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Optical Properties of Canopy Elements in Black Spruce, Jack Pine and Aspen Stands in Saskatchewan, Canada

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RÉSUMÉ

Les propriétés spectrales optiques (réflectance, R et absorbtance, A) ont été déterminées à partir de mesures en laboratoire de feuillage, de ramilles et d'écorce de tronc (R seulement) pour des peuplements forestiers boréaux avec des sous-étages arborescents en Saskatchewan (Canada). Ces sites incluent une plantation de pin gris (~15 ans) (Pinus Banksiana Lamb.) et trois peuplements matures (>60 ans) : pin gris, épinette noire (Picea mariana), et peuplier faux-tremble (Populus tremuloidus).

Des éléments du couvert supérieur et inférieur de l'étage forestier dominant et des sous-étages ont été étudiés, de juillet à la mi-septembre 1994, dans le cadre du projet BOREAS (Boreal Ecosystem-Atmospheres Study). Dans le cas des conifères, les aiguilles et l'écorce associées à une croissance en 1994 et des périodes variant de deux à cinq années précédentes ont été examinées. Un rapport de bandes (Rapport simple, SR, le rapport proche infrarouge/rouge) et la fraction du rayonnement photo-synthétiquement actif absorbé (fAPAR) ont été calculés à partir de spectres des surfaces foliaires adaxiales (au-dessus) et abaxiales (en dessous). On observe des différences significatives pour les paramètres optiques (R , fAPAR, et SR) entre les surfaces foliaires adaxiales et les surface abaxiales, et également au sein des espèces, des peuplements, des strates du couvert et au cours des saisons.

Les valeurs les plus élevées de fAPAR et de SR sont associées aux surfaces abaxiales des aiguilles des conifères mais inversement avec les surfaces adaxiales des feuillus. Des relations log-linéaires séparées entre SR et fAPAR sont nécessaires pour les feuillus, le pin et l'épinette noire. Les valeurs R des ramilles et de l'écorce sont similaires à celles du feuillage à de nombreuses longueurs d'ondes, se dégradant avec la classe d'âge dans la région du proche-infrarouge (PIR). Comparativement à l'épinette noire, les aiguilles de pin gris exhibent : une valeur de réflectance adaxiale inférieure dans le bleu (Rbleu), particulièrement au cours de l'automne; moins de saisonnalité dans les valeurs de réflectance adaxiale qu'abaxiale dans le visible (RVIS); des valeurs plus élevées de réflectance dans le proche-infrarouge (RPIR); et des valeurs plus élevées de fAPAR. Les valeurs de RPIR des aiguilles de pin gris (54 ± 3%) sont de 8- 10% plus élevées que pour le feuillage du peuplier faux-tremble ou de l'épinette noire. Des profils verticaux des paramètres optiques foliaires à travers la strate du couvert (3-4 couches) révèlent des patrons nettement différents pour les trois types de communauté (peuplier faux-tremble, épinette, pin gris) pour les valeurs de Rbleu adaxiale, RPIR adaxiale et de SR abaxial. Le seul paramètre optique montrant constamment une dégradation à travers le profil vertical dans tous les couverts est la RPIR abaxiale. Ces résultats devraient fournir des caractérisations optiques utiles pour la paramétrisation des simulations du transfert radiatif en forêt boréale.

SUMMARY

Spectral optical properties (reflectance, R and absorptance, A) were determined from laboratory measurements of foliage, and twigs and trunk bark (R only) in boreal forest stands having shrub understories in Saskatchewan, Canada. These sites included a plantation (~15 y) of jack pine (Pinus Banksiana Lamb.) and three mature stands (>60 y): jack pine, black spruce (Picea mariana), and aspen (Populus tremuloidus). Canopy elements from the upper and lower tree overstories and the understories were investigated from July through mid-September, 1994 as a part of the Boreal Ecosystem-Atmospheres Study (BOREAS). For conifers, needles and bark associated with growth in 1994 and two to five previous years were examined. A spectral ratio (Simple Ratio, SR, the

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near-infrared/red ratio) and the fraction of absorbed photosynthetically active radiation (fAPAR) were calculated from spectra of adaxial (upper) and abaxial (lower) foliar surfaces. Significant differences for optical parameters (R , fAPAR, and SR) were found for adaxial vs. abaxial foliar surfaces, and were also observed among species, stands, canopy strata, and season. The highest fAPAR and SR were associated with abaxial surfaces of conifer needles, but conversely, adaxial surfaces of broadleaves. Separate loglinear relationships between SR and fAPAR were necessary for broadleaves, pine, and black spruce. R of twig and bark was similar to foliage at many wavelengths, decaying with age class in the near-infrared (NIR) region. Compared with black spruce, jack pine needles exhibited: lower adaxial blue reflectance (R_{blue}), especially in autumn; less seasonality in adaxial vs. abaxial visible reflectance (R_{VIS}); higher near-infrared reflectance (R_{NIR}); and higher fAPAR. R_{NIR} of jack pine needles (54 ± 3%) was 8-10% higher than either aspen or black spruce foliage. Vertical profiles of foliar optical parameters through the canopy strata (3-4 layers) revealed distinctly different patterns for the three community types (aspen, spruce, jack pine) for adaxial R_{blue}, adaxial R_{NIR}, and abaxial SR. The only optical parameter to consistently demonstrate decay through the vertical profile in all canopies was abaxial R_{NIR}. These results should provide useful optical characterizations to parameterize radiative transfer simulations of boreal forests.

Keywords:
spectra, reflectance, *f*APAR, SR (Simple Ratio), adaxial/abaxial, BOREAS, jack pine, black spruce, aspen, overstory, understory.

Abbreviations:
The Boreal Ecosystem-Atmosphere Study, BOREAS; fraction of absorbed photosynthetically active radiation, *f*APAR; intensive field campaign (IFC), IFC-2 (July), and IFC-3 (late August/September); near-infrared radiation, NIR; "old aspen" study site, OA; "old black spruce" study site, OBS; "old jack pine" study site, OJP; reflectance in the visible spectrum, R_{VIS}; reflectance in the NIR spectrum, R_{NIR}; spectral absorptance A_λ ; spectral reflectance, R_λ ; spectral reflectance at 450 nm, 550 nm, 670 nm, and 800 nm – R_{450}, R_{550}, R_{670}, and R_{800}, respectively; Simple Ratio, SR, the ratio of R_{800}/R_{670}; spectral transmittance, T_λ ; visible radiation, VIS; wavelength, $_\lambda$; "young jack pine" study site, YJP.

INTRODUCTION

Land cover and forest inventories over large and essentially rural geographic regions are difficult to conduct and update unless they are based on spatial and categorical information of the type provided by satellite or aircraft observations. The most operational of these land cover assessment methodologies utilize optical remote sensing technology. In these, a "top-down" view of the landscape is provided at a variety of spectral, spatial, and temporal resolutions depending on the specific instrument and remote platform. Spectral, spatial and temporal patterns in the radiation scattered (or reflected) back from the landscape can be used to identify both type and state of land cover groups. For vegetation, dynamic aspects of state or condition may be inferred from reflectances, including average productivity, biomass and phenology of forests, grasslands, and other biomes.

The boreal region is an important component of the Canadian landscape, forming a patchwork quilt of bogs, agriculture, mature forest stands, and forest stands in various stages of recovery and succession following fires and logging. Boreal forests are dominated by needle-leaf coniferous species of genera such as *Pinus* and *Picea*. Broadleaf deciduous stands, primarily with species of the genus *Populus*, also are common – especially in the southern boreal range. Factors that influence species dominance in forest stands include type of soils/substrate, water table height and water availability to tree roots, average temperature and duration of the frost-free period, microclimate and topography. Boreal forests, in general, have relatively open canopies, so that the understory or substrate experiences both direct illumination and considerable shading from the tree overstory, due to the extreme solar incidence angles at latitudes >45°. While ferns and lichens often provide ground cover below coniferous stands, deciduous shrubs are common components of understories of both coniferous and deciduous stands, adding a distinctly seasonal phenological pattern to canopy reflectance. Interpretation of reflectances from these vertically and horizontally heterogeneous forests is difficult, since illuminated and shadowed contributions from the understory/substrate and the overstory are included in the canopy-integrated reflectances measured from above. However, canopy-integrated reflectances are dominated by scattering from the obliquely illuminated tree crowns of the upper canopy.

Interpretation of remotely acquired reflectances and simulation of radiative transfer in boreal forests require information on the optical scattering properties of foliage and other canopy elements within the vertical profile of forest canopies (Norman and Jarvis, 1974). Treetops typically are not sampled due to the difficulty of access (Williams, 1991), and understories ignored, when foliage is collected for optical measurements. Therefore, available information on optical properties of boreal species is sparse (Daughtry *et al.*, 1989), especially for canopy elements in the upper layers of mature tree overstories, and usually limited to reflectances (Carter *et al.*, 1989). Without transmittances, absorbed radiation cannot be directly determined, a severe constraint given the importance of the absorbed PAR fraction (*f*APAR). *f*APAR is a primary driver of photosynthetic processes in vegetation, influencing exchange of carbon, water, and nutrients between biomes and the atmosphere. Furthermore, measurements on adaxial (upper or dorsal) and abaxial (lower or ventral) foliar surfaces and needle age differences in conifers have recently been made possible with revised and rigorous methodologies (Middleton *et al.*, 1997a, Mesarch *et al.*, 1998).

Foliage and bark are important scattering elements in boreal forest stands. Spectral properties of foliage in the visible (VIS), or photosynthetically active radiation (PAR, 400 to 700 nm), spectrum are determined by leaf pigment content (Thomas and Gausman, 1977; Gausman, 1982), while near-infrared (NIR) reflectance is due to multiple refractions within leaf tissue (Wooley, 1971; Gausman, 1974). Leaf development alters foliar optical properties (Gausman *et al.*, 1970; Sinclair *et al.*, 1971), as does canopy position (Gausman *et al.*, 1970; Gausman, 1984), foliar age (Rock *et al.*, 1994; Wang *et al.*, 1995; Middleton *et al.*, 1997a), and nutrient or light limitations (Carter *et al.*, 1989). When morphological differences occur for adaxial and abaxial foliar surfaces, they influence optical properties (Walter-Shea *et al.*, 1989; Walter-Shea and Norman, 1990). Reflectance of newly formed (first year) conifer twigs is usually higher than for prior-year twigs, the decrease with age attributed to increased surface roughness (Williams 1991); spectral reflectances of twigs resemble soil spectra (increasing VIS, NIR reflectance with wavelength), except that young twigs show chlorophyll absorption at ~680 nm.

An ultimate and fundamental goal of the Boreal Ecosystem-Atmosphere Study (BOREAS) (Hall *et al.*, 1993; Sellers *et al.*, 1995a-c) was to obtain accurate estimates of canopy biophysical properties such as *f*APAR from remotely acquired optical observations. These optical properties provide the critical link between remotely acquired optical observations at canopy or landscape scales and leaf-level mass and energy exchange processes (Sellers *et al.*, 1992; Myneni and Williams, 1997; Loechel *et al.*, 1997). Therefore, correct interpretation of remotely acquired optical observations, or predicted biophysical parameters, of boreal forests depends on the accurate characterization of the optical properties of canopy elements, especially the foliage comprising the physiologically active canopy fraction. As participants in BOREAS, we have endeavoured to contribute to greater understanding of the optical characteristics within boreal forest canopies by collecting a unique data set of optical, morphological, and physiological data for tree overstories and their associated understories. We present a subset of that effort here, addressing the optical properties of foliage and bark for select sites.

METHODOLOGY

Study Sites and Species

The study was conducted at four boreal forest sites in Saskatchewan, Canada as part of BOREAS during the 1994 intensive field campaigns (IFCs). Measurements conducted in July (IFC-2) and early September (IFC-3) are reported here. The dominant overstory tree species per site were: black spruce (*Picea mariana* (Mill.) BSP) at a mature stand (>100 y; height ~10 m), referred to as the "old black spruce" site (OBS); quaking aspen (*Populus tremuloidus* Michx.) at a mature stand (~60 y; ht. ~20 m), referred to as the "old aspen" site (OA); jack pine (*Pinus banksiana* Lamb.) at a mature stand (~75 y, ht. ~15 m), known as the "old jack pine" site (OJP); and an establishing jack pine plantation (~15 y; ht. ~5 m), referred to as the "young jack pine" site (YJP). Stand characteristics are summarized in **Table 1**.

Optical properties were determined for foliage and bark from the upper and lower thirds of the overstory, referred to as canopy layers 1 and 2, respectively. Leaf optical properties of dominant understory plants were determined at three of four sites. At OBS, leaves in the upper strata of understory shrubs (referred to as layer 3) were examined for blueberry (*Vaccinium angustifolium* Ait.), wildrose (*Rosa woodsii*), and Labrador-tea (*Ledum groenlandicum* Oeder.), all of which formed clumps <1 m in height that were distributed irregularly above the moss/fern ground cover. At OA, leaf optical properties were determined in the upper and lower thirds (referred to as layers 3 and 4) of the hazelnut (*Corylus americana* Walt.) shrub understory, which formed a dense, continuous mat (horizontally and vertically) attaining a height $\leq$ 2 m. The understory shrub (layer 3) at YJP, bearberry (*Arctostaphylos Uva-ursi* (L.)

Table 1.
Characteristics of stands at four BOREAS study sites in Saskatchewan in 1994.

Site	Dominant Tree Species	Latitude, Longitude[1]	Age[2] (year)	Height[2] (cm)	Diameter[2] (cm)	LAI[2]	Density[2] (stem ha-[1])	Soil Texture[2]	Understory[3]
OBS	*Picea mariana*	53.99°N, 105.12°W	>100	10	8.8	5.6	6200	Organic	Rose, ledum, blueberry, mosses
OJP	*Pinus banksiana*	53.92° N 104.69°W	75	15	14.4	1.3	1200	Deep sand	Bearberry, mosses, lichens, alder
YJP	*Pinus banksiana*	53.85°N, 104.65°W	16	5	5.5	2.8	10700	Deep sand	Bearberry, bog cranberry, ryegrass
OA	*Populus tremuloides*	53.63°N, 106.20°W	60	21	17.9	3.3	1000	Sandy loam	Hazelnut, alder, shrubs

1. Steele, *et al*. (1997).
2. Lavigue and Ryan (1997).
3. Sullivan *et al*. (1997).

Spreng), was < 0.5 m tall and sparsely distributed over the grass ground cover (layer 4), which included a fuzzy-spiked wild rye (*Elymus innovatus* L.).

Sample collection

This was a collaborative study between two BOREAS research teams led by E. Middleton of NASA (Terrestrial Ecology Team #10, TE-10) and E. Walter-Shea of the University of Nebraska (TE-12), as summarized in **Table 2**. Overstory foliage and twig samples were taken from the upper and lower thirds of the tree canopies (layers 1, 2), while understory samples were taken from the shrubs/grass growing under the forest canopies (layers 3, 4). At the three mature sites, branches in the upper and lower overstory layers were accessed via platform towers (provided by BOREAS) that were placed ~100 m to 300 m from the instrumented towers. The young trees at YJP were sampled in a fixed area 100 m to 300 m from the instrumented tower (east of the access road). In general, five to ten replicate samples were acquired during each field campaign per species, canopy layer and age class.

Tree overstory foliage in canopy layers 1 and 2 were measured by TE-10 at all four sites during July and September, 1994. Optical measurements on aspen trunk bark (at OA) were made by TE-10 in July. At OBS, optical properties of twigs in the tree overstories were measured by TE-12 in mid-July (layer 2) and late August (layers 1 and 2), and on understory foliage at both times. At YJP, measurements were made by TE-12 on twigs (layer 1) and on understory foliage (layers 3 and 4) in mid-July and late August.

For leaf/needle overstory samples, branch tips were excised and placed in labeled, moist, zip-lock storage bags. A separate sample set was collected for twig measurements, consisting of small branch samples cut from the conifer trees, which were covered with damp cheesecloth and sealed in labeled, ziploc storage bags. Branchlet samples from the understory species were cut, the cut end placed in a water-filled vial immediately upon cutting, and the entire sample (with vial) sealed within ziploc storage bags. Aspen bark samples were removed from two trees (~20 m tall) that were harvested for biometry at OA. Samples were removed along vertical profiles on each trunk representing south-facing and north-facing aspects, at these relative tree heights (ht.): 15/16 ht, 7/8 ht, 3/4 ht, 1/2 ht, 1/4 ht, and at ~3 m.

All samples were placed on ice in coolers and transported to the field laboratory at Paddockwood School (Paddockwood, SK) for processing. Samples brought to the laboratory were refrigerated while awaiting handling. Needle subsets per age class (5 to 20 needles, depending on species) were removed from each sample and used for spectral optical property measurements, usually withing 4-6 h. Generally, twigs were processed (following conifer needle measurements) within two to three days of sampling. Understory and bark samples were processed within 24 h of collection. Individual leaves of understory broadleaf species at OBS and YJP were measured while attached to the branchlet held in the water-filled vial. Additional shoot-level characteristics were also measured, including leaf dimensions, projected foliar surface area and dry weight per age class, photosynthesis, and foliar biochemical constituents (Middleton *et al.*, 1997b).

Spectral optical properties were determined for both adaxial and abaxial surfaces of foliage (overstories and understories). The designation of foliar surfaces as either adaxial or abaxial was made on an anatomical basis (Esau, 1977). For broadleaves, the adaxial (upper, dorsal) surface is adjacent to the palisade mesophyll layer, while the abaxial (lower, ventral) surface is adjacent to the spongy mesophyll layer. For conifers, the adaxial surface is the flat (or less curved) facet whose surface lies closest to the xylem at the needle core, while the abaxial surface is the typically more curved and opposite facet whose surface lies closest to the phloem at the needle core.

Conifer needle and twig optical properties were obtained for three annual growth increments, or age classes (1, 2 and 3) which refer to shoot branching elements having needles expanded in the springs of 1994, 1993 and 1992, respectively. Since the development of twigs preceded needles by some number of

Table 2.
Measurement summary for sites, dates, and BOREAS teams.

Site/Canopy Stratum	IFC	Team	Date	Day of Year (DOY)
OBS				
Overstory	2	TE-10	July 28, Aug 03	209, 215
Understory	2	TE-12	Aug 03	215
Overstory	3	TE-10	Sep 13	256
Understory	3	TE-12	Sep 07	250
YJP				
Overstory	2	TE-10	July 22	203
Understory	2	TE-12	Aug 11	223
Overstory	3	TE-10	Sep 07	250
Understory	3	TE-12	NA	
OJP				
Overstory	2	TE-10	July 25	206
Understory	2	TE-12	NA	
Overstory	3	TE-10	Sep 06	249
Understory	3	TE-12	NA	
OA				
Overstory	2	TE-10	July 21, Aug 03	202, 215
Understory	2	TE-10	July 21	202, 215
Overstory	3	TE-10	Sep 02, Sep 12	245, 255
Understory	3	TE-10	Sep 02, Sep 12	245, 255

weeks/months, twig age was arbitrarily determined from the time of needle expansion in late May, 1994.

Optical Measurements

Foliar optical properties (reflectance, R_λ, and transmittance, T_λ, expressed in %) were determined from spectral measurements acquired using an integrating sphere (Li-COR 1800, Li-Cor, Inc., Lincoln, NE) mounted on a spectroradiometer (SE590, with >200 spectral channels in the visible and near-infrared spectra; Spectron Engineering, Denver, CO). A method similar to that of Daughtry *et al.* (1989) was used for broadleaves. A modification of the Daughtry *et al.* (1989) procedure for needles was adopted to enable measurements of both adaxial and abaxial surfaces and account for the inter-needle (and -twig) "gap fraction" that significantly influenced calculations of transmittances (T_λ) (Middleton and Walter-Shea, 1995; Middleton *et al.*, 1996, 1997a; Mesarch *et al.*, 1998). Only R_λ was obtained for twigs and bark.

Our revised methodology for the acquisition of spectral measurements combined an image analysis system with the standard hardware, comprised of the spectroradiometer, the integrating sphere, and one of two light sources (LI-1800-12 & LI-9918-011; LI-COR, Inc.) designed to produce either round or slitted illumination beams, respectively. These were paired with custom-made sample holders having either circular (for pine needles) or slitted (spruce needles) apertures. The image analysis system included a B/W CCD video camera, a monochrome frame-grabber board, an IBM PC compatible laptop unit with docking station, a light table, and a video monitor display with full 640 x 480 square pixel spatial resolution (pixel $= 1.11 \times 10^{-4}$ mm^2) and 256 gray levels. Software for image capture was "Computer Eyes/RT" (Digital Vision, Inc., Dedham, MA) and for processing was "Mocha" (Jandel Scientific, San Rafael, CA). Appropriate calibration procedures were used, including: a) for the stray light/dark current scans per measurement set; and b) for the wavelength stability of the radiometer and its spectral radiance coefficients, each field campaign. Custom software was developed (Mesarch *et al.*, 1998), to label, organize, document, and preprocess the spectral data acquired for T_λ and R_λ of adaxial and abaxial surfaces of each sample. These optical properties may be considered as directional-hemispheric reflectance or transmittance factors (at near-normal illumination).

The sample consisted of either leaves, needles from a single age class, twigs from a single age class, or bark (the outermost layer) mounted on a sample holder. For each sample, the percent R_λ (all samples) and T_λ (foliage only) was determined in the VIS and NIR regions (400-1000 nm). R_λ and T_λ of individual leaves of understory broadleaf species were measured while attached to the branchlet held in a water-filled vial. A spectral vegetation index known as the Simple Ratio (SR: NIR/Red, R_{800}/R_{670}) was calculated from reflectance spectra for each sample. For foliage, absorptance (A_λ) was calculated as $[100 - (R_\lambda + T_\lambda)]$. *f*APAR (expressed as a percent, %*f*APAR), was determined by integration of A_λ for the PAR region, as $[\int_{PAR} A_\lambda \, d\lambda] / [\int_{PAR} d\lambda]$. Reflectances and *f*APAR are reported here.

Data were organized by IFC, site, species, canopy layer, and age class. Statistical analyses were conducted using Systat 6.0 (SPSS Inc., Chicago, IL). Means were compared using the standard t-test. Vertical canopy profiles (layers 1-4) of leaf-level R_λ in three wavelengths – blue (450 nm, R_{450}), green (550 nm, R_{550}) and NIR (800 nm, R_{800}) – and the SR were examined at the three sites. The SR:*f*APAR relationship was examined for all measurements acquired.

Results

Leaf and Twig Spectra

Overstory and understory spectra at the OBS site. The reflectance spectra (R_λ) for black spruce needles and twigs acquired during the 1994 BOREAS field campaigns in midsummer (**Figure 1**) and in early autumn (**Figure 2**) are shown for the three youngest annual growth increments (age classes 1 to 3, from 1994 to 1992, respectively). Differences in adaxial versus abaxial foliar surface R_λ were evident at both times of the growing season, and in both the upper and lower strata (layers 1 and 2) of the black spruce overstory (**Figures. 1a,b** and **2a,b**). Abaxial surfaces had lower R_{VIS} and higher R_{NIR} than adaxial surfaces; consequently, significantly higher ($P \leq 0.01$) overall means (averaged over season and age classes) for the SR (R_{800}/R_{670}) were produced for abaxial (6.7 ± 0.3) versus adaxial (4.2 ± 0.4) needle surfaces. The greatest black spruce needle adaxial/abaxial distinction occurred in the blue spectrum during autumn (**Figure. 2**), when a 30% increase in adaxial R_{450} (from ~11% to ~15%) over summer values occurred (**Figures. 1** and **2**; **Table 3**).

The youngest black spruce twigs (age class 1) had relatively high R_{NIR} (~50%), equivalent to (or exceeding) the most highly reflective abaxial needle surfaces (~47%). In fact, R_λ of age class 1 twigs exceeded that of needles and older twigs at VIS/NIR wavelengths >550 nm. Twig R_λ declined significantly with age class, especially in the NIR. For example, R_{NIR} in young twigs (~50%, age class 1) was higher than in older twigs (30 to 40%, age classes 2 and 3). In addition to the NIR, older twigs were considerably less reflective than needles in the blue/green (<600 nm) spectrum. Needle R_λ also declined with age, especially for adaxial surfaces, but this effect was more subtle than for twigs and is treated more extensively elsewhere (Middleton *et al.*, 1997a). In the lower spruce canopy, there was less variation in R_{NIR} for needles, especially during autumn (**Figure. 2b** versus **2a**).

Understory shrubs at OBS showed seasonal, species, and adaxial/abaxial R_λ differences (**Figure 3 a,b**). Blueberry and wildrose leaves (**Figure 3a**), and fully mature new leaves (age class 1) of Labrador tea (**Figure 3b**), had similar adaxial R_{VIS} spectra. However, species differences were pronounced for abaxial spectra, especially for R_{VIS}. In July, wildrose had ~4% higher adaxial R_{NIR} and ~8% higher abaxial R_{VIS} than blueberry; these two species had more similar abaxial spectra in early autumn. R_{VIS} were quite variable for the two contemporaneous leaf age classes (1 and 2) of the evergreen shrub (Labrador tea), and temporal dynamics per foliar surface type and age class were complicated. Spectra for several leaf categories resembled

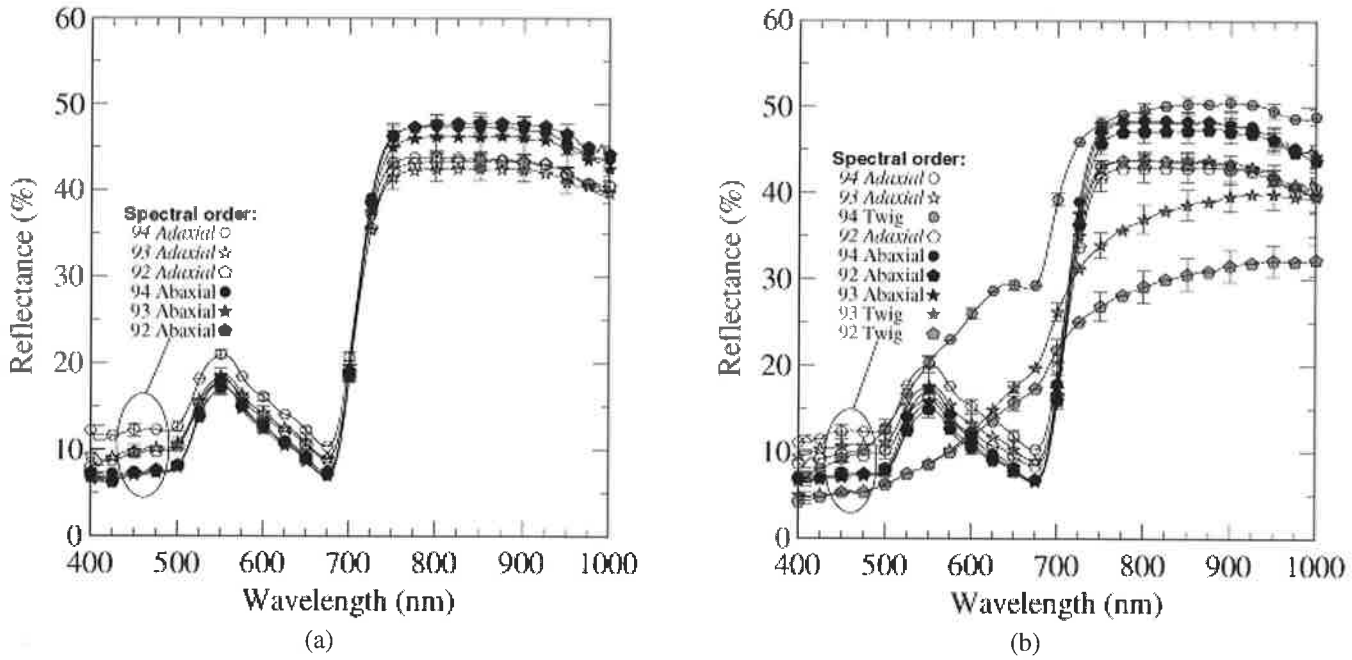


Figure 1.
Reflectance spectra are shown for black spruce needles and twigs acquired from the overstory at the BOREAS OBS site in Saskatchewan during July 1994: (a) upper canopy, needles only; and (b) lower canopy, needles and twigs. Three age classes are given : new growth (○), one -year old growth (☆), and two-year old growth (⌂). Symbol filling indicates media examined: filled symbols = abaxial (ventral) foliar surfaces; open symbols = adaxial (dorsal) foliar surfaces; and shaded symbols = twigs. Spectra were originally obtained with a sampling increment of 3 nm, but were subsampled at 25 nm increments for presentation; error bars indicating ±SE are provided at 50 nm increments. The legend within the figure indicates the order (highest to lowest reflectance) for these needle and twig spectra, at a selected wavelength.

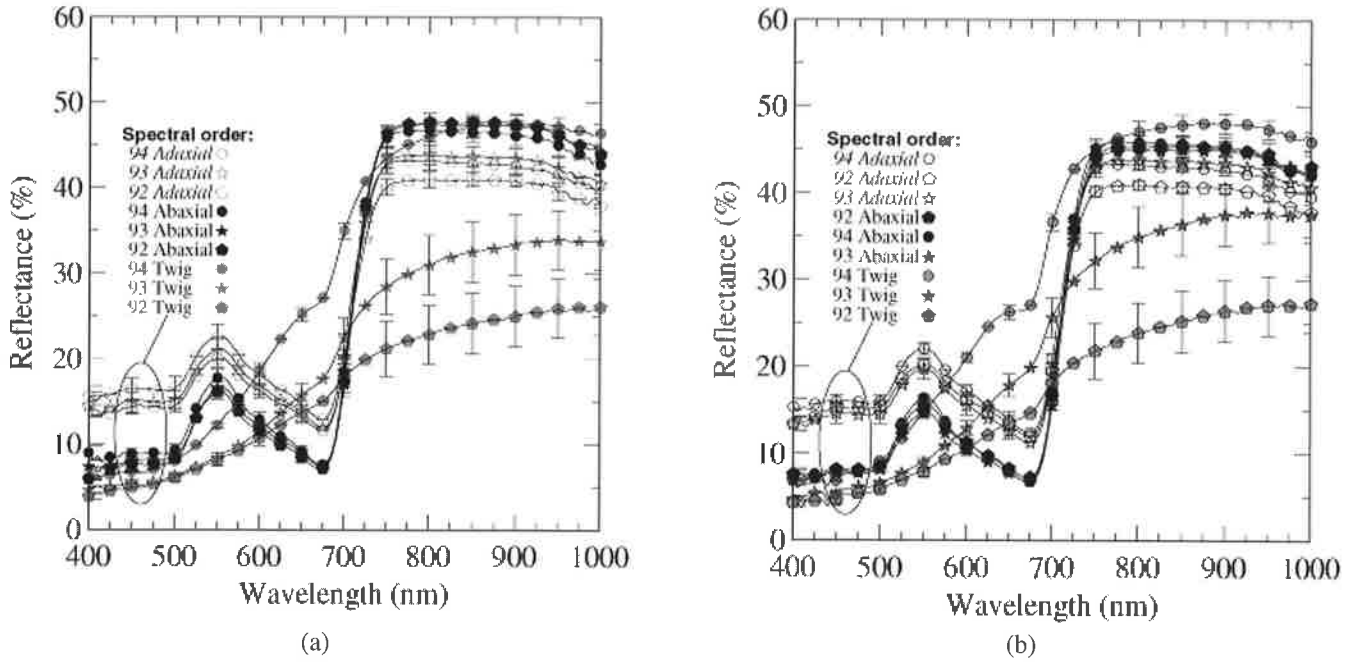


Figure 2.
Reflectance spectra are shown for black spruce needles and twigs acquired from the overstory at the BOREAS OBS site in Saskatchewan during early September 1994: (a) upper canopy, needles and twigs; and (b) lower canopy, needles and twigs. Three age classes are given: new growth (○), one-year old growth (☆), and two-year old growth (⌂). Symbol filling indicates media examined: filled symbols = abaxial (ventral) foliar surfaces; open symbols = adaxial (dorsal) foliar surfaces; and shaded symbols = twigs. Spectra were subsampled, as described in Figure 1, with error bars provided at 50nm increments, indicating ±SE. The legend within the figure indicates the order (highest to lowest reflectance) for these needle and twig spectra, at a selected wavelength.

Table 3.

Vertical profiles of four optical parameters assimilated from measurements of mulitple canopy strata[1] at four boreal sites[2] in summer and fall: adaxial foliar values[3].

Optical Parameter	Canopy Stratum	OBS		OJP		YJP		OA	
		July Mean (±SE)	Aug/Sept Mean (±SE)	July Mean (±SE)	Aug/Sept Mean (±SE)	July Mean (±SE)	Aug/Sept Mean (±SE)	July Mean (±SE)	Aug/Sept Mean (±SE)
Blue Reflectance, R_{450}	1	10.6 (0.4)d	15.2 (0.2)e	7.2 (0.2)b	8.0 (0.2)c	7.3 (0.3)b,c	7.5 (0.2)b,c	4.7 (0.1)a	5.8(0.3)a
	2	11.0 (0.6)d	15.2 (0.5)e	6.7 (0.2)b	8.2 (0.2)c	6.8 (0.2)b	6.9 (0.2)b	5.2 (0.4)a	5.9 (0.3)a
	3	6.2 (4.0)a,b	4.9 (0.4)a	----------	----------	----------	6.6 (0.2)b	4.9 (0.1)a	6.4 (0.2)a
	4	----------	----------	----------	----------	----------	11.6 (0.4)d	4.9 (0.1)a	5.6 (0.2)a
Green Reflectance, R_{550}	1	19.2 (0.5)d	21.2 (0.8)c,d	19.6 (0.7)c,d	20.6 (0.3)e	18.8 (0.6)c,d	19.6 (0.4)d	9.6 (0.9)a	22.5 (2.8)e,f
	2	11.0 (0.6)a	15.2 (0.5)b	17.0 (0.5)c	18.7 (0.3)d	18.0 (0.6)c,d	18.7 (0.5)d	10.6 (0.9)a	22.9 (2.6)e,f
	3	13.7 (5.0)a,b,c	12.3 (1.4)a,b	----------	----------	----------	17.8 (0.2)c	13.2 (0.6)a,b	27.7 (2.1)f
	4	----------	----------	----------	----------	----------	24.1 (0.6)f	14.5 (0.5) b	17.8 (1.6)c,d
NIR Reflectance, R_{800}	1	42.8 (0.6)a	42.7 (0.7)a	54.8 (0.9)d,e	57.2 (0.4)e	56.3 (0.6)d,e	57.6 (0.5)e	47.8 (0.3)b	47.5 (0.4)b
	2	43.6 (0.6)a	42.7 (0.5)a	53.1 (0.9)d	55.3 (0.6)d	56.7 (0.9)d,e	54.9 (0.8)d,e	47.7 (0.3)b	47.2 (0.1)b
	3	47.4 (2.0)a,b	44.9 (1.5)a,b	----------	----------	----------	49.0 (0.4)c	47.8 (0.5)b	47.5 (0.4)b
	4		----------	----------	----------	----------	47.3 (0.7)b	43.9 (0.4)a,b	44.5 (0.7)a,b
SR (NIR/Red Ratio)	1	4.7 (0.1)b	3.5 (0.1)a	6.9 (0.1)c	6.2 (0.1)c	7.3 (0.2)c,d	7.0 (0.1)c	10.4 (0.3)e	2.9 (1.6)a,b
	2	4.9 (0.3)b	3.6 (0.1)a	7.5 (0.1)d	6.4 (0.2)c	7.7 (0.1)d	7.4 (0.2)c,d	9.4 (0.6)e	3.1 (1.4)a,b
	3	7.2 (1.2)c,d	7.6 (0.2)d	----------	----------	----------	7.8 (1.4)d,e	9.1 (0.6)e	5.9 (1.2)b,c
	4	----------	----------	----------	----------	----------	4.5 (1.1)a,b	8.4 (0.5)d,e	5.3 (1.1)b,c

1. Values for canopy layer 3 (the understories) are averaged over species at OBS and YJP.
2. Values for conifers are averaged over all age classes available per site (1990-1994).
3. Statistically different means ($P \leq 0.05$) per spectral parameter (R_{450}, R_{550}, R_{800}, and SR) are designated with different lower case letters.

those of young twigs (**Figures 3b** versus **2a**), due either to loss of chlorophyll or to a colour change in the abaxial pubescence (from a soft silvery green to rust/orange) after overwintering. R_{NIR} for Labrador tea (>50% in summer, ~45% in early autumn) exceeded that of the spruce overstory.

Overstory and understory spectra at the two Pine sites. There were few influences of foliar surface (adaxial/abaxial), needle age, or seasonal change on R_λ of jack pine needles at YJP (upper canopy, **Figure 4 a,b**). There were also no significant foliage reflectance differences associated with upper and lower canopy strata at YJP (spectra not shown). Leaf spectra for the ryegrass groundcover and bearberry shrub were similar in August (**Figure 4c**), except that R_{VIS} of the adaxial > abaxial surface – as was seen for conifer needles. R_{NIR} (~48% ± 2%) in both understory species was 8 to 10% lower than that of the pine overstory; R_{VIS} for the understory foliage was ≥ 5% higher than overstory needles.

In contrast to the situation at YJP, reflectance of pine needles at the OJP site exhibited canopy position effects (R_λ, upper > R_λ, lower) throughout the VIS/NIR spectra in mid-summer (**Figure 5**; **Tables 3**, **4**). For example, R_{550} of both adaxial and abaxial surfaces were higher ($P \leq 0.05$) in canopy layer 1 during summer. In autumn, needles in canopy layer 2 at OJP (**Figure 5 a,b**) also exhibited increased R_{550} for both foliar surfaces (**Tables 3** and **4**) and increased R_{450} for abaxial surfaces. Foliar R_{NIR} in summer for OJP (~53.5%) was lower ($P \leq 0.05$) than at YJP (~56%), but was equal at the two sites in autumn. A greater contrast existed between needles of the two coniferous species – pine versus black spruce. Summer R_{NIR} (53 to 57%) of jack pine needles was significantly higher ($P \leq 0.01$) than black spruce needles (43 to 48%); adaxial R_{450} was lower ($P \leq 0.001$) in jack pine than black spruce needles, especially in autumn (pine, ~7%; spruce, 15.2%). In general, the OJP values were intermediate to those of YJP and OBS.

For jack pine (YJP only) and black spruce, twigs of age class 1 had similar R_{NIR} (**Figure 4** versus **Figures 1**, **2**); but black spruce twigs (age class 1) had considerably higher R_{VIS} (≥ 20%). The low R_{VIS} of jack pine twigs was comparable to R_λ of needles in the 600-700 nm range. Twigs of both coniferous species showed an R_λ decline with age class that was most pronounced in the NIR. This decay in NIR reflectance was linear with the logarithm of twig age (**Figure 6**):

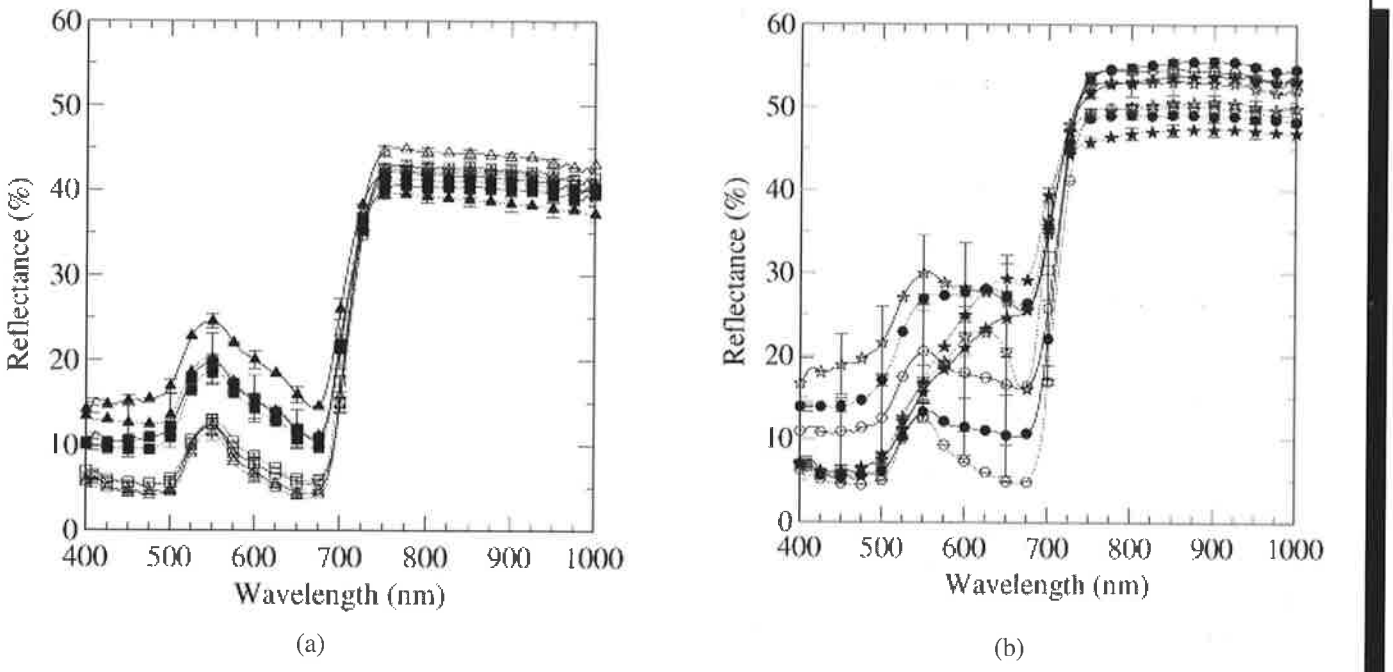


Figure 3.
Reflectance spectra are shown for leaves of three species comprising the upper stratum of the understory at the BOREAS OBS site in Saskatchewan during July (solid lines) and late August (dashed lines) of 1994, for adaxial (open symbols) and abaxial (filled symbols): (a) two deciduous shrub species, rose and blueberry; symbols indicate species, wildrose (△) and blueberry (□); and (b) Labrador tea, a broadleaf evergreen; symbols indicate new leaves (○) or one-year old leaves (☆). Spectra were subsampled, as described in Figure 1, with error bars provided at 50 nm increments, indicating ±SE.

a) for jack pine twigs ($r^2 = 0.96$),
$R_{NIR}(\%) = 55.5 - 9.8*\log(\text{Twig Age})$; and
b) for black spruce twigs ($r^2 = 0.93$),
$R_{NIR}(\%) = 59.2 - 9.8*\log(\text{Twig Age})$.

Overstory and understory spectra at the OA site. Reflectance spectra for leaves and bark at the OA stand are given in **Figure 7a-c**. In the aspen overstory (**Figure 7a**) where R_{NIR} was 45 to 50%, no differences due to canopy strata (canopy layers 1 and 2), leaf surface (adaxial versus abaxial), or seasonal change were apparent for leaf R_λ (i.e., all aspen NIR spectra were equal). However, adaxial versus abaxial surfaces and seasonal change strongly influenced R_{VIS} in aspen leaves, with both factors influencing reflectance to about the same extent (**Figure 7a**). There were also no differences in R_{VIS} in the upper/lower layers of the aspen overstory. The summer abaxial spectra of aspen leaves were most similar to those of black spruce needles. R_{NIR} of jack pine needles (54% ± 3%) was ~8 to10% higher than either aspen leaves (45% ± 4%) or black spruce needles (44% ± 3%); R_{VIS} of jack pine needles (and the abaxial surfaces of black spruce needles) were intermediate between the values obtained for aspen's adaxial and abaxial surfaces.

Bark from the aspen trunk (**Figure 7b**) showed considerable spectral differences due to canopy position. R_λ for bark in the treetop (layer 1>17 m) and on the lower trunk (layer 3, ~3 m) were comparable on the north- and south-facing trunk. R_{NIR} was similar (860 nm peak, ~65%) for these two trunk regions, although R_{VIS} was lower in the treetop than on the lower trunk (R_{550} ~17% versus 24%). In the treetop, the R_{VIS} of bark and leaves were similar. In the lower trunk, R_{VIS} of bark was usually >5% higher than leaves, except for abaxial foliar surfaces in autumn. In the mid-trunk (canopy layer 2), R_{VIS} for the north-facing bark was similar to that of lower trunk bark (<25%), while R_{VIS} for the south-facing bark was considerably more reflective (R_{550} = 47%).

Adaxial/abaxial and seasonal differences were evident for foliage in the understory hazelnut shrub (**Figure 7c**), although not as strongly expressed as in the aspen overstory. In both aspen and hazelnut, abaxial R_{VIS} > adaxial R_{VIS}, and R_{VIS} in autumn was greater than R_{VIS} in summer – especially in the chlorophyll absorption range between 525 – 700 nm (**Figure 7a**, **b**). In contrast to the aspen overstory, the hazelnut understory exhibited leaf surface influences on R_{NIR} (adaxial > abaxial), and some differences in R_{NIR} associated with upper/lower canopy position (layer 3 > Layer 4, **Figure 7c**). In comparing the R_{NIR} of the overstory and understory, hazelnut < aspen for abaxial surfaces; only the adaxial surfaces of hazelnut leaves from the upper shrub layer had R_{NIR} as high as aspen leaves. In summer, hazelnut's adaxial and abaxial spectra were similar to those of shrubs at OBS (**Figures**. **3a** versus **7c**) – except for Labrador tea (**Figure 3b**). R_{VIS} for hazelnut foliage in autumn was similar to bearberry (YJP) in August; R_{NIR} for bearberry foliage was ~5% higher than for hazelnut, and closer to the pine overstory value (hazelnut at OA, 38% to 42%; bearberry, 47% to 50%; pine, 55% to 60%).

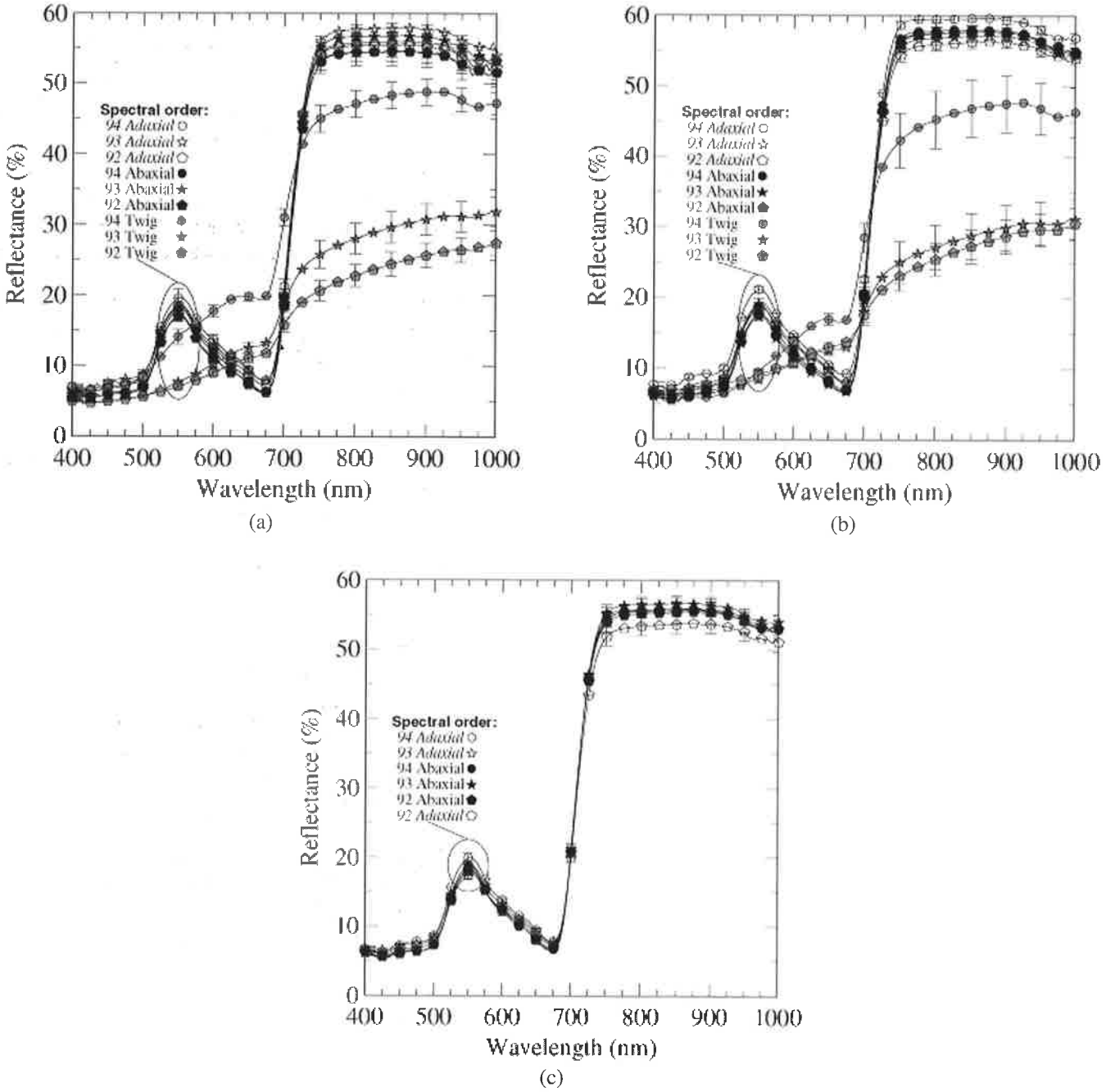
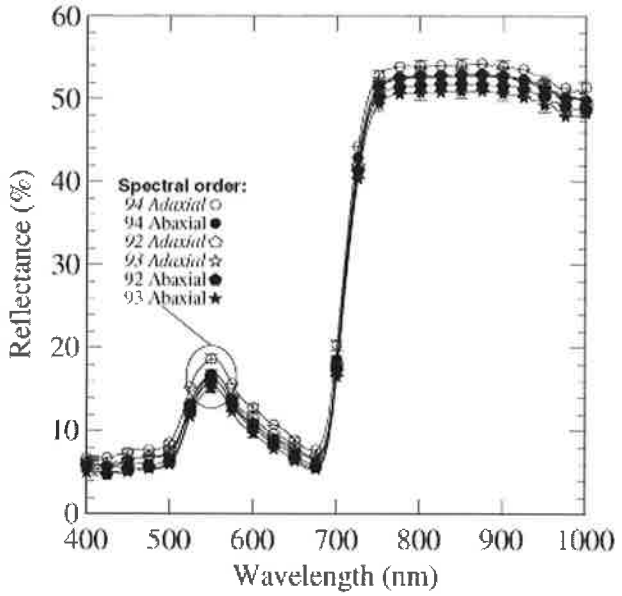


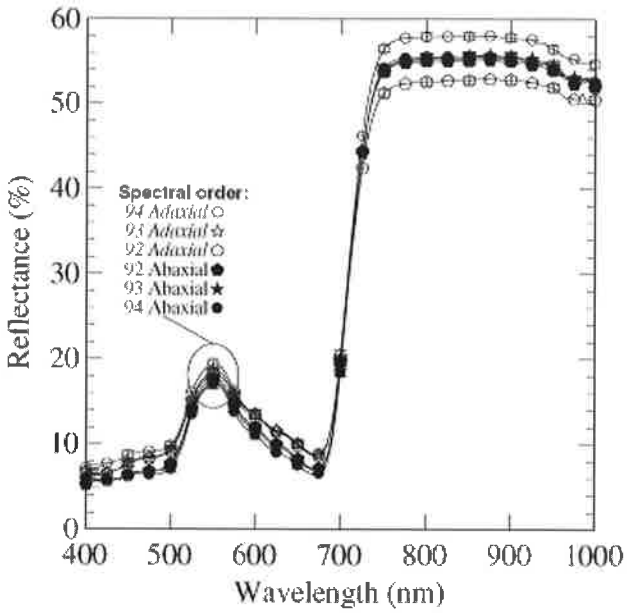
Figure 4.
Reflectance spectra are shown for jack pine needles and twigs acquired from the overstory and the understory at the BOREAS YJP plantation site in Saskatchewan: (a) upper overstory layer, July 1994; and (b) upper overstory layer, September 1994; and (c) understory leaves of two species, grass (□) or bearberry (△). For the overstory, three age classes are given: new growth (○), one-year old growth (☆), and two-year old growth (⌂). Symbol filling indicates media examined: filled symbols = abaxial (ventral) foliar surfaces; open symbols = adaxial (dorsal) foliar surfaces; and shaded symbols = twigs. No twig measurements were acquired in the lower canopy. Needle reflectances in the lower overstory were similar to those in the upper layer (spectra not shown). Spectra were subsampled, as described in Figure 1, with error bars provided at 50 nm increments indicating ±SE. The legend within the figure indicates the order (highest to lowest reflectance) for these needle and twig spectra, at a selected wavelength.

Spectral Reflectance Profiles for Canopy Elements at the Boreal Sites

We organized our foliage and twig/bark R_λ according to canopy layer, designating the upper and lower overstory as layers 1 and 2, and designating the upper and lower understory as layers 3 and 4 (**Tables 3**, **4**). Different vertical profile patterns (from top to bottom of the forest stand) for adaxial and abaxial R_{450}, R_{550}, R_{800} (**Figures 8** to **10 a,b**), and SR (**Figure 11**) were revealed at the four sites. The values given for the understory at OBS (layer 3) represent the average for the three



(a)



(b)

Figure 5.
Reflectance spectra are shown for jack pine needles acquired from the overstory at the BOREAS OJP site in Saskatchewan: (a) lower canopy, in July; and (b) lower canopy, in September. Three age classes are given: new 1994 growth (○), one-year old 1993 growth (☆), and two-year old 1992 growth (△). Symbol filling indicates media examined: filled symbols = abaxial (ventral) foliar surfaces; open symbols = adaxial (dorsal) foliar surfaces; and shaded symbols = twigs. Spectra were subsampled, as described in Figure 1, with error bars provided at 50 nm increments indicating ±SE. The legend within the figure indicates the order (highest to lowest reflectance) for these needle and twig spectra, at a selected wavelength.

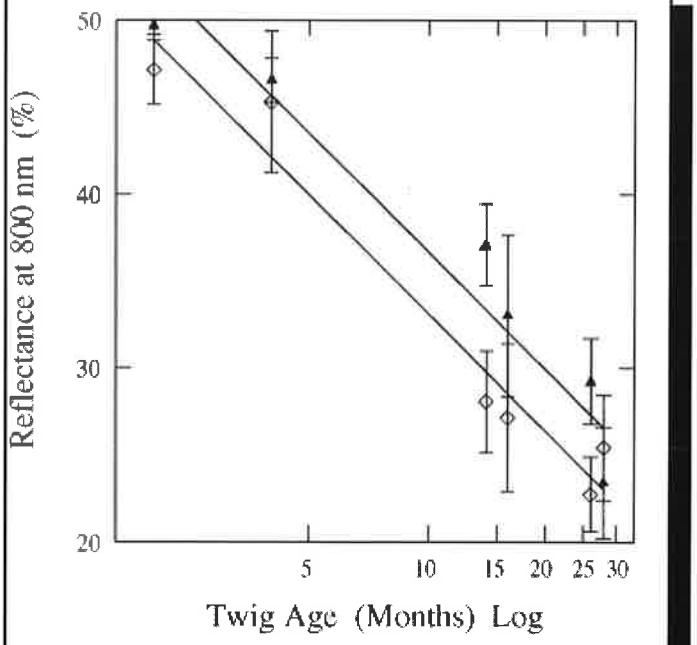


Figure 6.
The log-linear decay in twig NIR reflectance (800 nm) with age is given for jack pine (◇) and black spruce (▲). Error bars indicate ±SE. Equations are:

a) jack pine twigs (r^2 = 0.96), R_{NIR} reflectance = 55.5 − 9.8*log (Twig Age);
b) black spruce twigs (r^2 = 0.93), R_{NIR} reflectance = 59.2 − 9.8*log (Twig Age).

shrubs; the values given for the conifer overstory elements are the average for the three age classes.

Blue reflectance profiles for foliage. The optical profile most successful for discriminating among black spruce, jack pine, and aspen sites, even with seasonal differences, was adaxial R_{450}. The highest adaxial R_{450} was produced by black spruce foliage at OBS, with a relatively large seasonal increase compared to jack pine at the two sites or aspen (**Figure. 8a**; **Table 3**). However, abaxial R_{450} for aspen was almost twice that of pine foliage (aspen, ~11%; jack pine, ~6%), with intermediate values for black spruce (**Figure 8b**; **Table 4**). There were no significant differences in R_{450} in the two overstory layers at any site.

For the fully deciduous canopy at OA, adaxial and abaxial R_{450} were relatively constant through the four strata (**Figure 8a,b**; **Tables 3**, **4**); the onset of senescence produced relatively small autumn increases. Very different profiles, as compared to the fully deciduous OA site, were observed at sites having a coniferous overstory and a deciduous understory (OBS, YJP) which yielded significant overstory versus understory contrasts. This was because adaxial surfaces of foliage in the conifer overstories and the grass ground cover had higher R_{VIS}, but the leaf undersides were more reflective in the shrubs (canopy layer 3). Adaxial R_{450} (~5 to 7%) for the shrub understories ≤ the conifer overstories, while abaxial R_{450} of the understory (~10 to14%) always exceeded conifer values. At YJP, adaxial R_{450} was similar for pine and its shrub understory (~7%), but was much higher for the grass groundcover (11.6% ± 0.4%). Abaxial R_{450} for the shrub understories were much greater than

Table 4.

Vertical profiles of four optical parameters assimilated from measurements of multiple canopy strata[1] at four boreal sites[2] in summer and fall: abaxial foliar values[3].

Optical Parameter	Canopy Stratum	OBS		OJP		YJP		OA	
		July Mean (±SE)	Aug/Sept Mean (±SE)	July Mean (±SE)	Aug/Sept Mean (±SE)	July Mean (±SE)	Aug/Sept Mean (±SE)	July Mean (±SE)	Aug/Sept Mean (±SE)
Blue Reflectance, R_{450}	1	6.7 (0.1)c	8.2 (0.3)d	5.8 (0.1)a	6.4 (0.1)b,c	5.9 (0.1)a,b	6.3 (0.1)b,c	10.7 (0.2)e	12.8 (0.5)f
	2	7.4 (0.2)c,d	7.9 (0.2)d	5.4 (0.1)a	6.3 (0.1)b,c	5.8 (0.2)a	6.2 (0.1)b	10.1 (0.2)e	13.2 (0.8)f
	3	14.0 (5.0)a-f	12.1 (3.5)d,e,f	-------	-------	-------	10.9 (0.4)e	10.1 (0.3)e	14.0 (0.4)f
	4	-------	-------	-------	-------	-------	6.9 (0.2)c	10.2 (0.3)e	11.3 (0.3)e,f
Green Reflectance, R_{550}	1	6.7 (0.1)a	8.2 (0.3)b	18.6 (0.5)d,e	18.6 (0.3)d	17.4 (0.4)c,d	17.9 (0.3)c,d	21.4 (0.5)e	31.0 (1.8)f
	2	17.5 (0.5)c	16.8 (0.5)c	16.0 (0.4)c	17.3 (0.2)c	16.9 (0.4)c	18.2 (0.3)d	20.7 (0.4)e	30.9 (1.8)f
	3	23.9 (7.0)c-f	21.9 (4.0)c-f	-------	-------	-------	25.1 (1.0)e	21.3 (0.5)e	29.9 (1.2)e,f
	4	-------	-------	-------	-------	-------	19.7 (0.7)d,e	21.3 (0.4)e	23.2 (0.7)e
NIR Reflectance, R_{800}	1	46.7 (0.9)c	47.3 (0.7)c	54.3 (0.5)d	56.2 (0.3)d	55.2 (0.8)d	57.7 (0.3)d	46.8 (0.3)c	46.4 (0.3)c
	2	47.9 (0.6)c	45.4 (0.6)c	51.7 (1.0)d	55.4 (0.4)d	55.2 (0.7)d	55.8 (0.6)d	46.2 (0.3)c	46.2 (0.3)c
	3	47.1 (5.2)b,c	44.1 (2.1)b,c	-------	-------	-------	47.7 (0.8)c	41.6 (0.4)b	40.5 (0.4)a,b
	4	-------	-------	-------	-------	-------	45.4 (0.6)c	39.0 (0.4)a	40.6 (0.5)a,b
SR (NIR/Red Ratio)	1	6.7 (0.2)c,d	6.3 (0.2)c	8.3 (0.1)e	7.8 (0.1)d,e	8.7 (0.2)e,f	8.4 (0.1)f	4.3 (0.4)b	2.0 (1.1)a
	2	7.2 (0.2)d	6.5 (0.1)c	9.1 (0.1)g	8.1 (0.1)e	8.8 (0.2)e,f	8.4 (0.1)f	4.5 (0.3)b	2.1 (1.0)a
	3	3.4 (1.0)a	3.8 (0.9)a	-------	-------	-------	4.0 (2.1)a,b	3.6 (0.4)a	2.8 (0.8)a
	4	-------	-------	-------	-------	-------	6.5 (0.6)c	3.3 (0.4)a	2.7 (0.6)a

1 Values for canopy layer 3 (the understories) are averaged over species at OBS and YJP.

2 Values for conifers are averaged over all age classes available per site (1990-1994).

3 Statistically different means ($P \leq 0.05$) per spectral parameter (R450, R550, R800, and SR) are designated with different lower case letters.

for their conifer overstories at OBS and YJP. For shrubs at OBS and OA, adaxial R_{450} in layer 3 (upper understory) was considerably higher than comparable values in layer 4 (layer 3 >> layer 4).

Green reflectance profiles for foliage. Seasonal and site differences characterized the R_{550} profiles. Adaxial R_{550} (unlike R_{450}) was significantly higher in canopy layers 3 and 4 than in the conifer overstory (layers 1 and 2) in both summer and fall (**Figure 9a,b**). In autumn, adaxial R_{550} declined throughout the full canopy at OBS. The reverse profile occurred at OBS for abaxial R_{550}, which increased greatly from top to bottom of the canopy (**Table 4**). The lowest abaxial R_{550} was produced by black spruce needles in the upper overstory (~7%). But, abaxial R_{550} in summer/fall essentially remained constant (~17%) in the pine overstory layers (i.e., less change than adaxial surfaces). In spite of these different trends, abaxial R_{550} was similar (16 to 19%) in layer 2 at all coniferous sites.

At OA, in contrast to the conifer stands, adaxial R_{550} was higher in the shrub understory than in the tree overstory in summer (**Figure 9a**; **Table 3**). The lowest adaxial R_{550} (~10%) was associated with the upper aspen canopy, which increased greatly in autumn (~23%) to exceed values observed at the conifer sites (summer/fall, ≤ 21%). In summer, adaxial R_{550} was similar (~13%) for the understories (layer 3) at OBS and OA. Abaxial R_{550} in layers 3 and 4 was 20 to 26% at all sites (except OA in autumn) (**Figure 9b**; **Table 4**). At OA, abaxial R_{550} was similar across all layers in summer (~21%) and across the upper three layers in autumn (~31%); the autumn foliage produced the highest abaxial green reflectance among sites.

NIR reflectance profiles for foliage. Adaxial R_{800} profiles were distinctly different for black spruce, jack pine, and aspen stands (**Table 3**). Abaxial R_{800} profiles (**Figure 10b**; **Table 4**) were the most striking, in that they showed either declining values through the canopy layers (YJP in autumn, OJP in summer, OA in summer/fall, and OBS in fall) or no change (OBS in summer, 47% ± 1%; YJP in summer, 55% ± 1%). A declining profile was the general trend for R_{800} in the pine canopies in July and September. Abaxial R_{800} for aspen and black spruce was equal in the upper canopy (layer 1) in both summer and fall; in layer 2, abaxial R_{800} was equal for black spruce in autumn and aspen in summer.

R_{800} for pine (52 to 58%) was always higher than other groups (black spruce, aspen, or understory species), with the greatest species separation achieved with adaxial measurements.

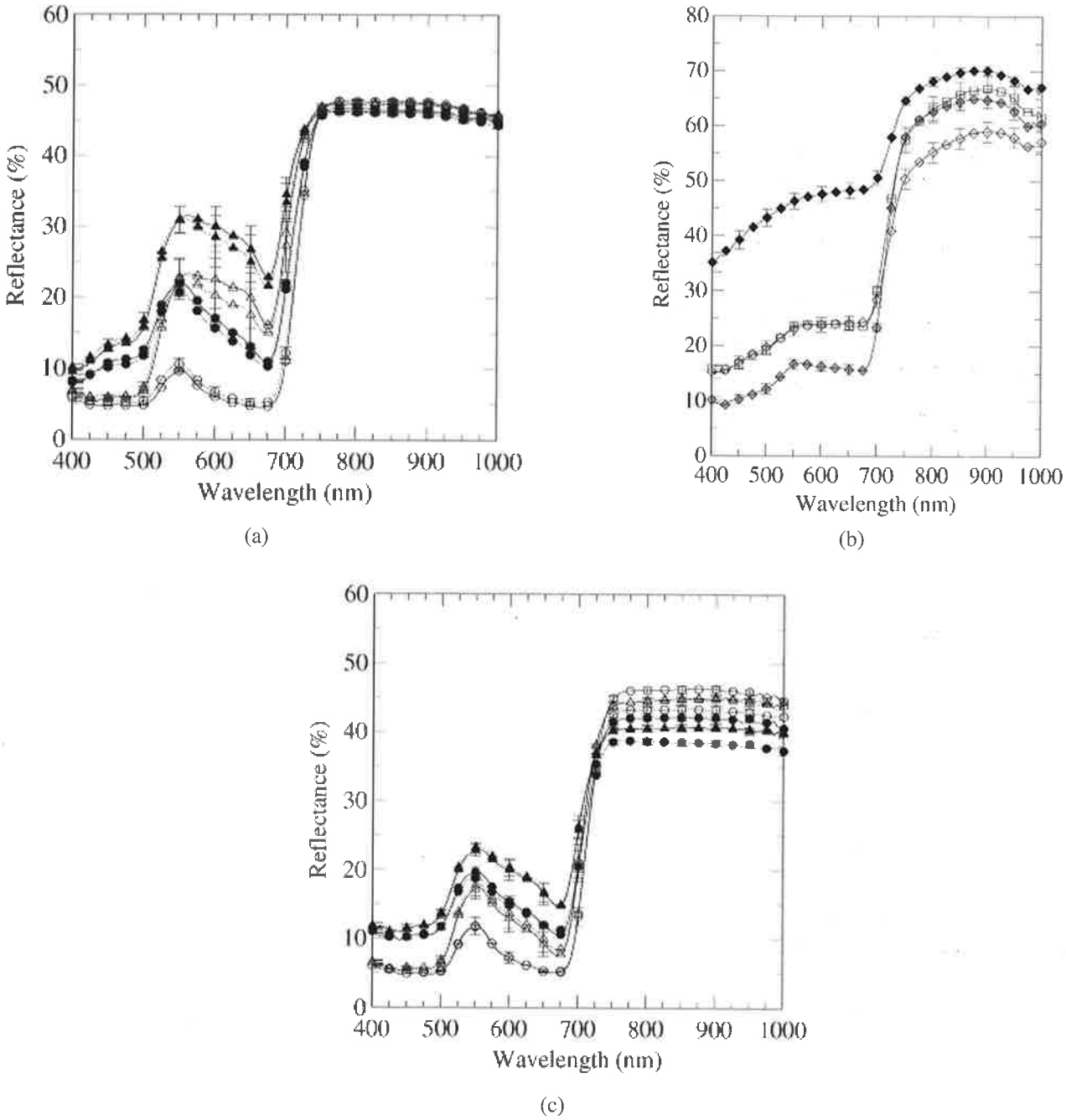


Figure 7.
Reflectance spectra are given for foliage and trunk bark of the aspen tree overstory and hazelnut shrub understory at the OA site during July (IFC-2, ○) and September (IFC-3, △): (a) aspen (layer 1, solid line; layer 2, dashed line); (b) aspen trunk bark in the upper overstory (layer 1, ◇ hatched), in the mid-trunk region (layer 2: south-facing side, ◇; north-facing side, ♦), and in the lower trunk (layer 3, □); and (c) hazelnut (layer 3, solid line; layer 4, dashed line); For foliage, abaxial (ventral) = filled symbols, and adaxial (dorsal) surfaces = open symbols. Spectra were subsampled, as described in Figure 1, with error bars indicating ±SE provided at 50 nm increments.

The lowest adaxial R_{800} (~43%) was observed in the black spruce overstory, which had a more reflective understory (45 to 48%). Intermediate adaxial R_{800} occurred at OA, where summer and fall profiles were identical – constant (47-48%) over the upper three layers, dropping to ~44% in the lower understory (layer 4). Abaxial profiles were similar at OA in summer and fall (**Table 4**).

SR profiles for foliage and bark. A comparison of the SR in the four overstories (OA, OBS, YJP, OJP) shows that significant differences ($P \leq 0.01$) were associated with adaxial versus abaxial foliar surfaces, seasonal change, and in some cases, canopy position (**Figure 11 a,b**). For all deciduous broadleaves examined, adaxial SR > abaxial SR; however, the reverse was true for the conifers and the grass ground cover (abaxial SR >

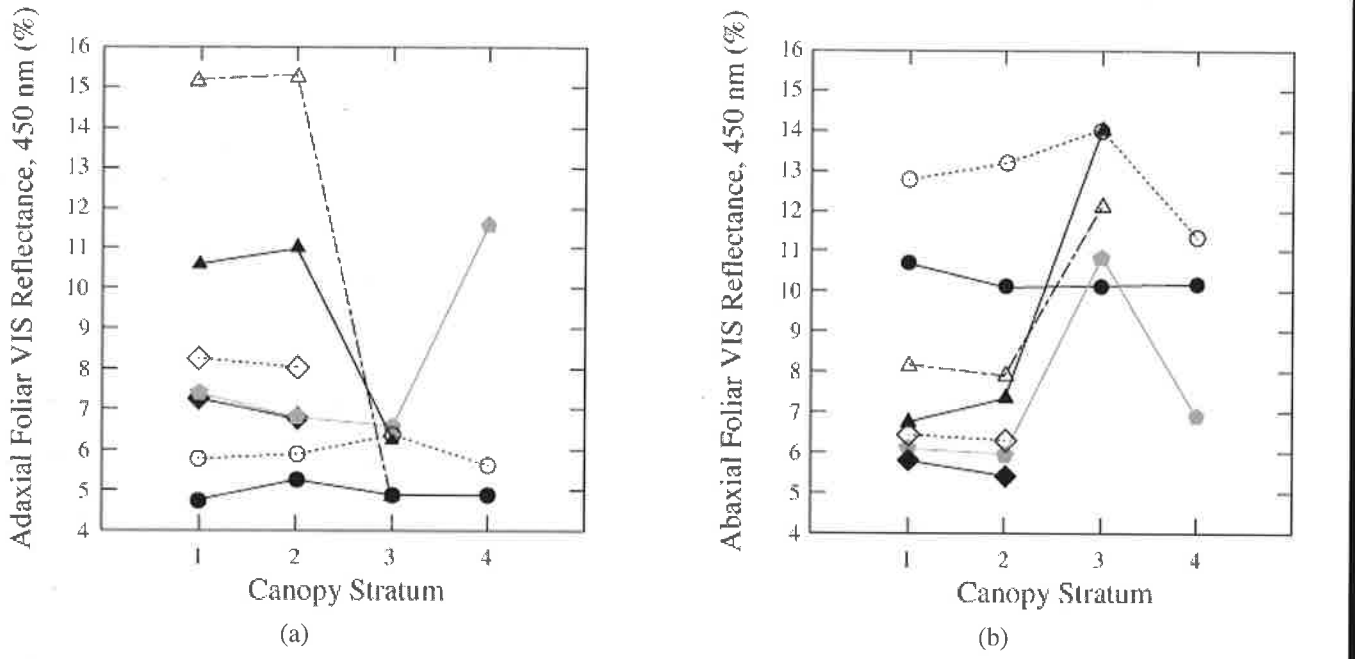


Figure 8.
Canopy vertical blue reflectance [R_{450}] profiles are given for foliar optical properties (averaged over age classes) at four boreal sites in summer (filled symbols, solid lines) and autumn (open symbols, dashed lines): (a) adaxial (dorsal) foliar surfaces; and (b) abaxial (ventral) foliar surfaces. Symbols indicate site: OBS (△); OA (○); OJP (◇); and YJP (⌂).

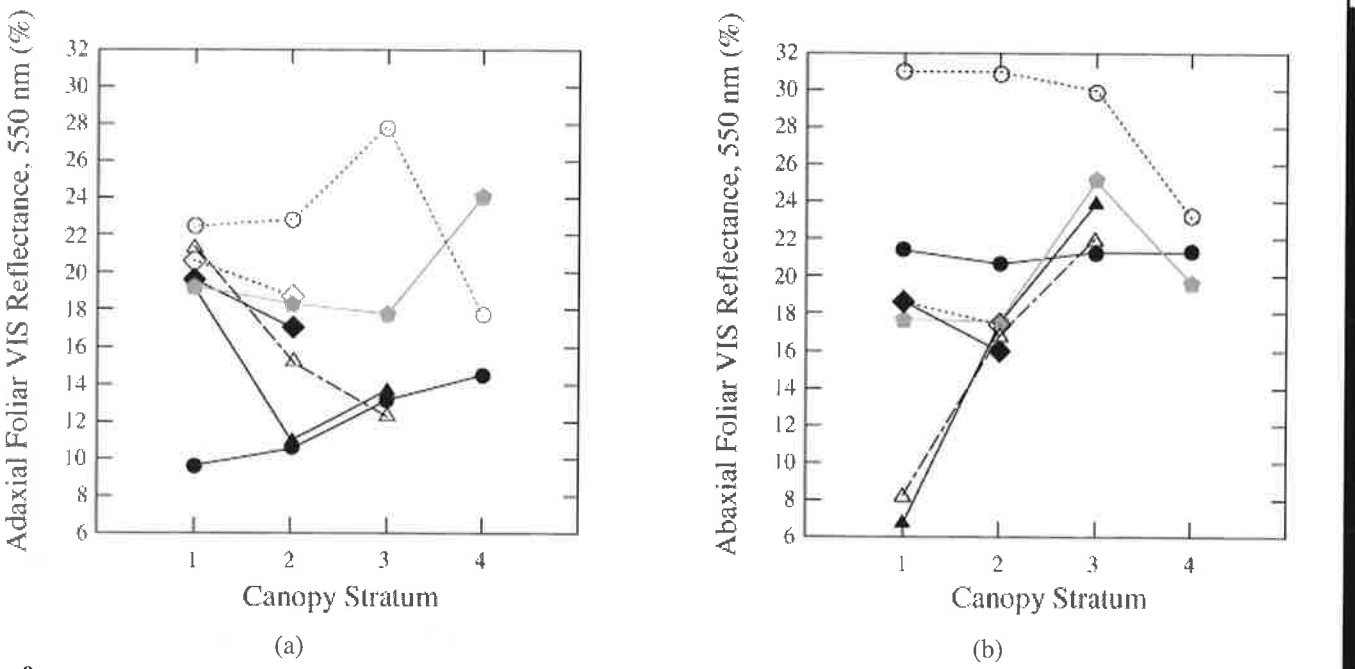


Figure 9.
Canopy vertical green reflectance [R_{550}] profiles are given for foliar optical properties (averaged over age classes) at four boreal sites in summer (filled symbols, solid lines) and autumn (open symbols, dashed lines): (a) adaxial (dorsal) foliar surfaces; and (b) abaxial (ventral) foliar surfaces. Symbols indicate site: OBS (△); OA (○); OJP (◇); and YJP (⌂).

adaxial SR). Canopy profiles and magnitudes for adaxial and abaxial SR were vastly different among the boreal sites (**Figure 11 a,b**; **Figure 12 a,b**). However, SRs (adaxial, abaxial) were equal in the two overstory layers at all sites. In the treetops (layer 1) at OA, SR for aspen trunk bark was equal to abaxial SR of aspen leaves in summer. All other aspen bark SRs (mid-trunk, lower trunk) and twig SRs (black spruce and jack pine) were similar to abaxial SR of senescent aspen leaves in autumn (**Figure 11B**).

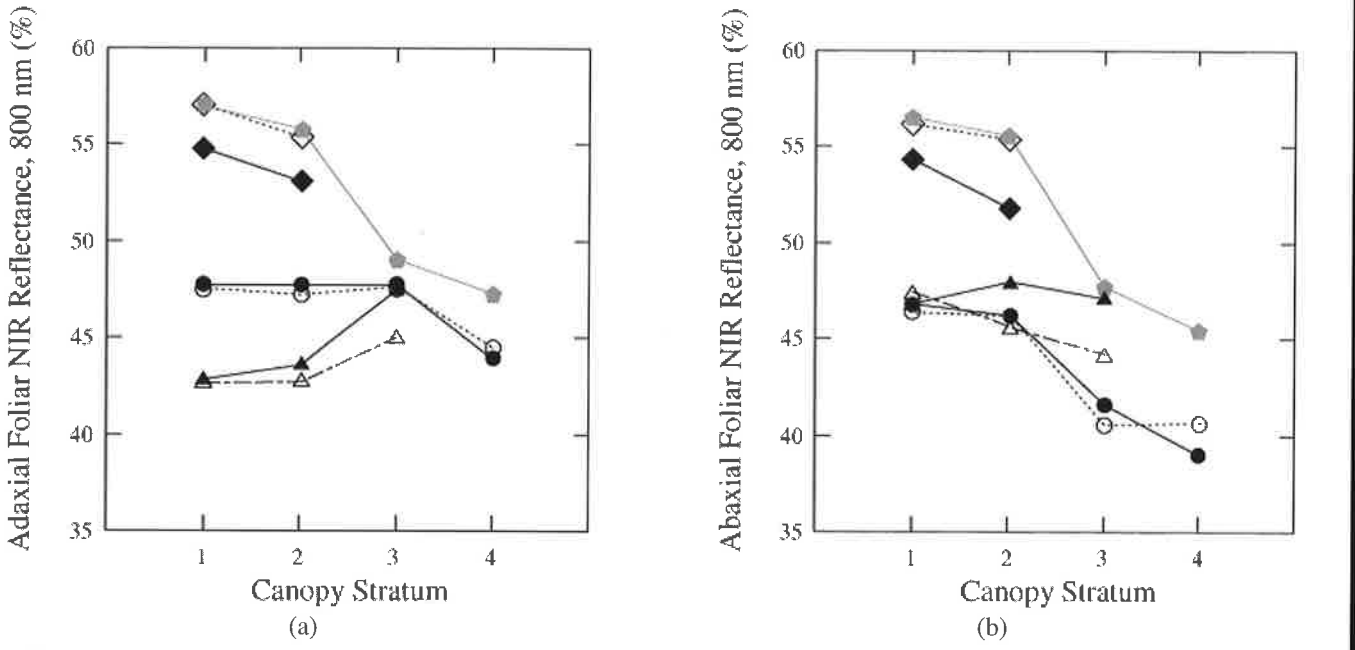


Figure 10.
Canopy vertical NIR reflectance [R_{800}] profiles are given for foliar properties (averaged over age classes) at four boreal sites in summer (filled symbols, solid lines and autumn (open symbols, dashed lines): (a) adaxial (dorsal) foliar surfaces; and (b) abaxial (ventral) foliar surfaces. Symbols indicate site: OBS (△); OA (○); OJP (◇); and YJP (⌂).

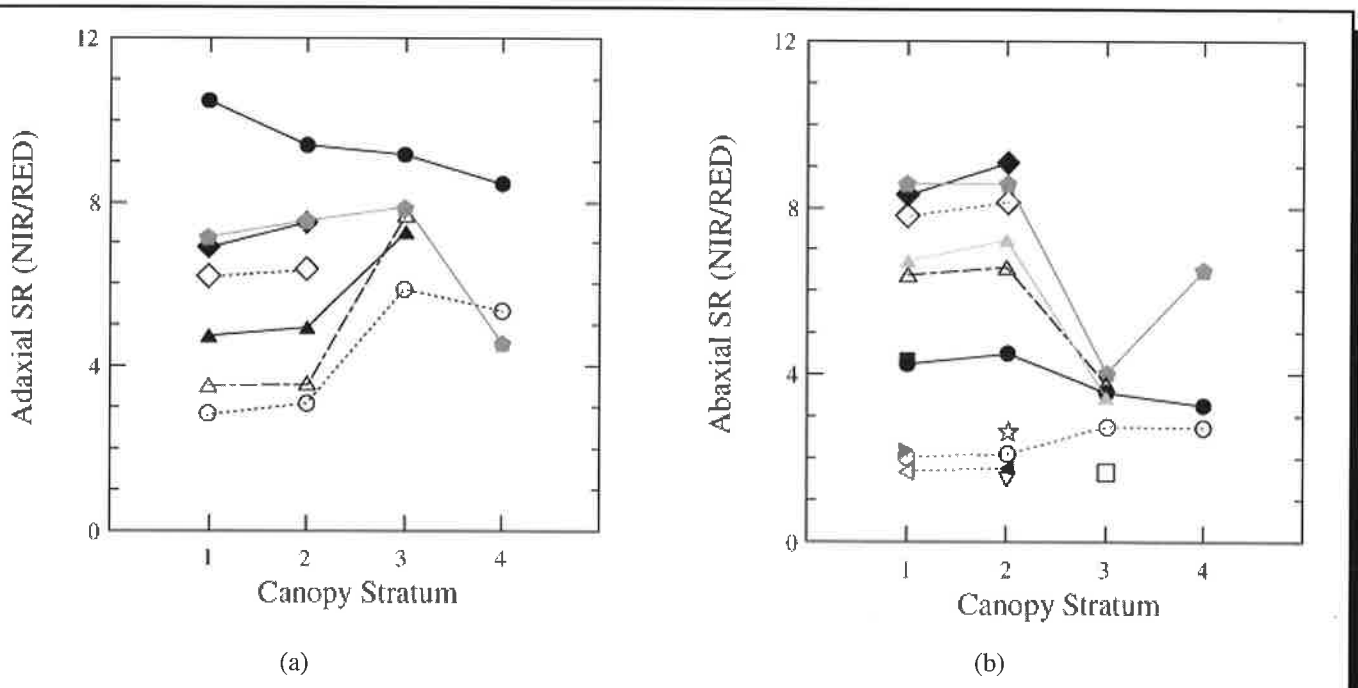


Figure 11.
Canopy vertical profiles for the SR [R_{800}/ R_{670}] are given for foliar and twig/bark optical properties (averaged over age classes) at four boreal sites in summer (filled symbols, solid lines) and autumn (open symbols, dashed lines): (a) adaxial (dorsal) foliar surfaces; and (b) abaxial (ventral) foliar surfaces, plus twig/bark values. Symbols indicate site and media: foliage at OBS (△); OA (○); OJP (◇); and YJP (⌂); twigs at OBS (◁), twigs at YJP (▷), bark at OA (average for north/south facing, □; north-facing, ☆; south-facing, ▽).

The highest adaxial SRs were produced by aspen (~10) and hazelnut (~8) in summer at the deciduous site (OA), with significant decline within the canopy profile. The next highest adaxial SRs (7 to 8) were produced by the jack pine overstories (YJP, summer/fall; OJP, summer only) and the shrub understories at the conifer sites (OBS, YJP). In autumn, both black spruce needles (3.5 ± 0.1) and senescent aspen leaves (3.0± 1.5) had the lowest adaxial SR of the tree ovestories. As expected, a

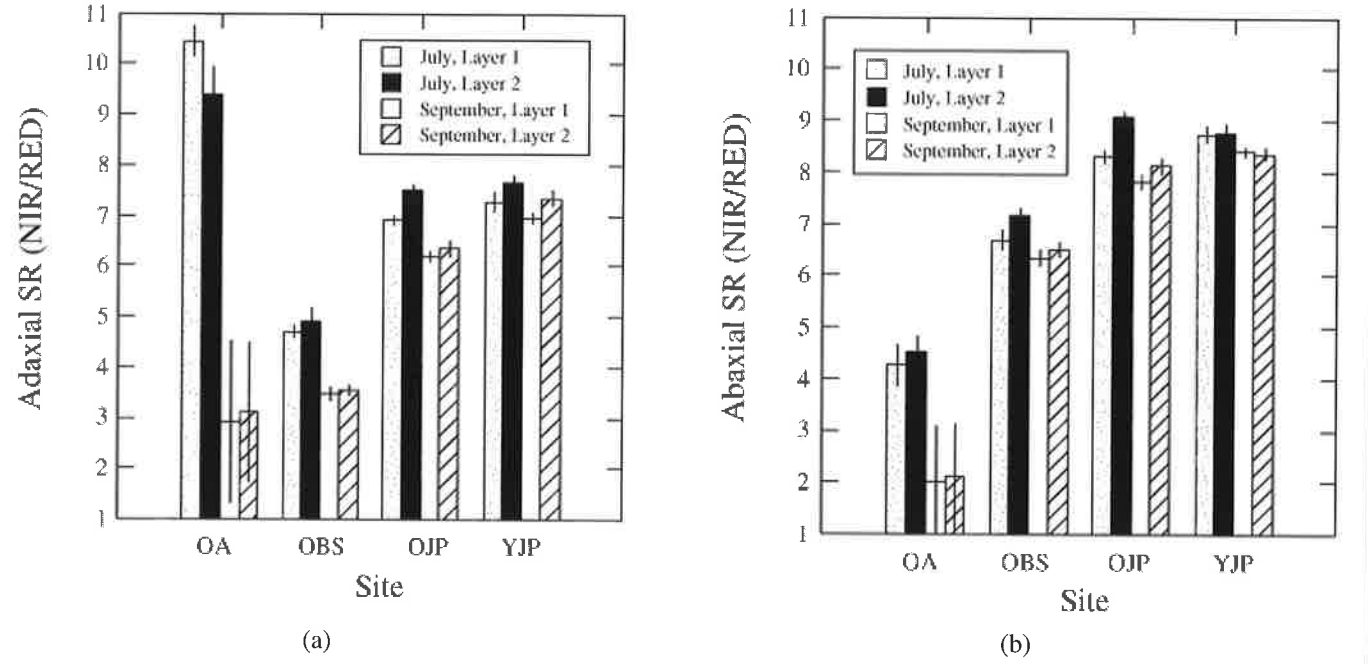


Figure 12.
The SRs for the four boreal overstories (aspen, black spruce, and jack pine at YJP and OJP) are given for the foliage from the upper and lower canopies during summer and autumn (IFC-2 and IFC-3). Data for conifers were averaged over age classes: (a) SR calculated from adaxial (dorsal) reflectances; and (b) SR calculated from abaxial (ventral) reflectances. IFC-2 = grey-tone bars and IFC-3 = open bars; the lower overstory layer = hatched bars, the upper layer = "no hatch". Error bars indicate ±SE.

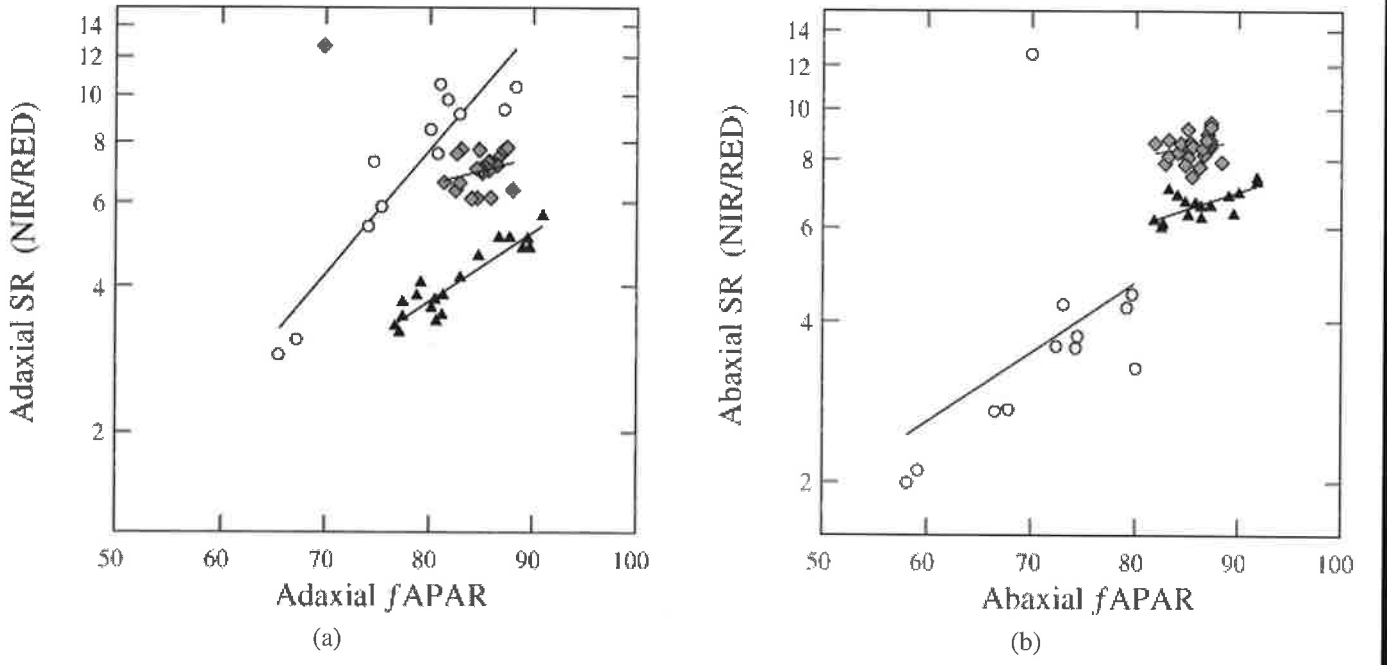


Figure 13.
The SR for foliage as a loglinear function of *f* APAR is given for deciduous species, jack pine, and black spruce: (a) adaxial measurements; and (b) abaxial measurements. Equations are:

a) adaxial surface, deciduous broadleaves (○), aspen, hazelnut, grass, blueberry, rose, and bearberry, logSR = 0.59(*f*APAR) - 2.648 (r^2=0.86).
b) abaxial surface, deciduous broadleaves (○), logSR=0.053(*f*APAR) -1.861 (r^2=0.76).
c) adaxial surface, black spruce (▲), logSR = 0.033 (*f*APAR) - 1.357 (r^2 =0.88).
d) abaxial surface, black spruce (▲), logSR = 0.014 (*f*APAR) + 0.644 (r^2 =0.69, with significant effect for canopy position, P=0.015).
e) no significant relationship for jack pine (◇).

large seasonal reduction in SR occurred at OA, but reductions also occurred in autumn at OJP and OBS. Adaxial SR for the understory > tree overstory at OA (autumn) and OBS (summer/fall). Adaxial (4.5) and abaxial (6.5) SR for grass resembled black spruce (and not the higher values associated with its YJP overstory).

A different order was obtained for abaxial SR of the boreal overstories, with conifers exceeding aspen (**Figure 12b**; **Table 4**). In fact, distinct profiles for black spruce, jack pine, and aspen were obtained with abaxial SR. Abaxial SR was highest at the pine sites (8-9), followed by black spruce (6.3 to 7.2; summer > fall in layer 2), aspen in summer (~4.4), and aspen in autumn (~2.0). Abaxial SR for all understory shrubs $\leq$ 5 (i.e., all deciduous broadleaf values were similar). Seasonal changes were captured in abaxial SR, but were less pronounced than seasonal changes in adaxial SR. Furthermore, equivalent adaxial SRs were obtained for aspen and black spruce foliage in autumn, and equal SRs were obtained for aspen (abaxial) and black spruce (adaxial) SRs in summertime (**Figures 11, 12**). Adaxial and abaxial SRs were significantly higher in layer 2 (compared to layer 1) at OJP. In autumn at OA, SRs (especially adaxial) were higher in the hazelnut understory than in the aspen overstory.

Relationship of SR to *f*APAR

When the general relationship of SR to *f*APAR (both determined from reflectances) was examined, separate loglinear relationships were apparent across species groups (**Figure 13 a,b**). For deciduous species, neither species (except ledum), canopy layer nor seasonal (summer/fall) differences were important; when adaxial and abaxial surfaces were pooled, $r^2 = 0.66$ (data not shown). For deciduous measurements, stronger relationships were obtained when the foliar surfaces were examined separately: adaxial ($r^2 = 0.86$) and abaxial ($r^2 = 0.76$). Separate relationships for adaxial ($r^2 = 0.88$) and abaxial ($r^2 = 0.69$, with significant canopy position effect, P=0.015) measurements were also obtained for black spruce. Although the measurements for jack pine formed distinct clusters distinguishable from black spruce and deciduous species, no significant relationship between SR and *f*APAR was observed.

Discussion

The measurements in this project document foliar optical properties (R_λ, *f*APAR) for tree overstories and shrub understories, supplemented by bark and twig reflectances from overstory elements, of boreal forest stands during the summer and autumn of one growing season during BOREAS. We determined R_λ as influenced by: canopy position; seasonal and age-related changes in needles and twigs of conifers; seasonal change in deciduous leaves in an aspen stand; and seasonal change in the shrub understories of conifer stands. These measurements were acquired to characterize expected changes in canopy element optical properties over the experimental period, and to provide optical parameters for radiative transfer and physiological process models for the BOREAS sites. Our measurements complement *in situ* reflectance measurements made above the forest understories at many of the BOREAS sites (Miller *et al.*, 1997) and remotely acquired observations of these stands.

In model simulations, foliar reflectance and spectral vegetation indices (e.g., SR) are used as indicators of plant physiological vigor (e.g., Sellers *et al.*, 1992). Our measurements highlight the complexity within the vegetative canopies for heterogeneous sites such as BOREAS, which may lead to difficulties in inferring vegetation attributes from canopy-integrated, remotely obtained spectra from such sites. Radiative transfer models that account for species composition, and relative abundance of canopy elements (e.g., "mixture" models; Myneni and Williams, 1997; Chen and Leblanc, 1997; Kimball *et al.*, 1997), should be more successful in scaling from individual foliar elements to shoots, branches, canopies and landscapes, given the temporal and vertical profile dynamics of foliar (and twig) reflectance. In conifer stands, the age of the canopy element also influences the reflectance property (e.g., twigs had linear decay of R_{800} with age).

From the "above canopy" remote sensing perspective, reflectance contributions from the adaxial surfaces of foliage are most important since these are the surfaces that typically dominate the view from above. Radiative transfer simulations typically use a single spectral parameterization (e.g., adaxial SR or R_{NIR}) for foliage within a canopy to describe leaf influences on scattering properties. Our profiles of spectral optical properties at four boreal forest stands clearly show species, site, and/or canopy position differences for R_λ and SR, with substantial differences depending on whether the adaxial or abaxial foliar surface is evaluated. Although these profiles do not provide the actual reflectance contribution per canopy layer to the total canopy optical parameter, they do provide an indicator of the potential contribution on an equal leaf area basis for canopy components per canopy stratum. The rendering of the integrated reflectances from canopy elements into canopy-level reflectance as measured from tram or aircraft will be highly dependent on the plant element selected to represent a particular species, and successful description of the architecture of the canopy elements (including clumping), and shadows in lower strata. Species differences among the tree overstories were distinctly expressed in the adaxial NIR spectra, but no species influences on NIR parameters were evident in the understories across sites. Overstory species differences were especially distinct in the adaxial blue spectrum, influencing both site and seasonal changes; however, R_{blue} contributions from shrubs and grass were similar or greater than R_{blue} from the overstory, potentially compromising vegetation classification accuracy. Species differences among the tree overstories, and site-specific profiles, were also captured in the abaxial SR. Use of the adaxial SR to produce canopy-level estimates of energy of matter exchanges could be strongly biased by the presence of understory foliage ($\geq$ overstory values).

Adaxial and abaxial morphological differences are well-known adaptations to regulate foliar energy balance, reducing the impact of environmental conditions such as high illumination and drought (diurnal or seasonal). In broadleaves, adaxial/abaxial morphological differences are typically manifested in

the development of a leaf underside that has lower chlorophyll content, and appears brighter and whiter in the PAR spectrum. These morphological adaptations are especially effective if coupled with leaf movements that reduce exposure to solar illumination of photosynthetic tissue – more strongly associated with adaxial surfaces of broadleaves, such as occurs in the twisting of "quaking" aspen leaves in even slight breezes. Adaxial/abaxial differences occur in broadleaf shrubs for similar reasons, and also because they may be exposed to high radiation and/or drought early or late in the growing season when their phenology differs from the overstory (e.g., earlier leaf-out for hazelnut than aspen). Below a relatively open boreal coniferous overstory, shrub foliage may receive relatively high illumination. Consequently, increased exposure of abaxial foliar surfaces in all canopy layers to direct solar illumination and to remote sensors viewing the stand from above may occur.

We have also recently provided the most rigorous available optical characterizations of both adaxial and abaxial foliar surfaces of conifer needles (Middleton *et al.*, 1997a), and continue that investigation here. We show that adaxial/abaxial spectral differences were significant for foliage of all conifer stands examined, with the greatest differences exhibited by black spruce foliage. In contrast to broadleaves, the "greener" surface of conifers is the abaxial underside. Since the abaxial surfaces of conifer needles had consistently higher SR than adaxial surfaces, they also attained higher *f*APAR (and presumably its associated mesophyll contributed more to photosynthetic processes) than adaxial surfaces. This morphology may represent an adaptation to protect tissue with higher photosynthetic potential from direct irradiation over the wide range of conditions that occur throughout the year. Therefore, the "brighter" (for R_{VIS}) adaxial surfaces of coniferous shoots typically face upward, and are the dominant surfaces captured in the remote view.

In broadleaf forests, the remote sensing of adaxial surfaces has been successfully used to infer canopy-level photosynthetic potential, or physiological vigour. However, for coniferous forests, a significant underestimate of photosynthetic potential using remote sensing algorithms (e.g., Earth Observing System, Running *et al.*, 1996) could result if only adaxial R_λ values, rather than an appropriate mix of adaxial and abaxial values, are used in radiative transfer simulations linked to physiological models. This error will be compounded if the relationship for broadleaves is used to predict *f*APAR from SR in conifers (**Figure 13**). We have shown elsewhere (Middleton *et al.*, 1997b) that the fundamental leaf-level loglinear relationship between SR and *f*APAR is optimally described when SR is determined from foliar transmittance, and is qualitatively different for deciduous and coniferous species. Here we examined the leaf-level relationship between SR (determined from foliar reflectance) and *f*APAR, again finding that deciduous and coniferous species must be separately considered; coniferous species tend to have a higher *f*APAR ($\leq$ 85%) at a given SR (based on reflectance), but the predictive strength of the SR:*f*APAR relationship among conifers is much stronger for some groups (e.g., black spruce) than others (e.g., jack pine). When determined from reflectances, the SR was not useful for predicting *f*APAR in jack pine; however, adequate correlations for jack pine were demonstrated previously when these optical parameters were determined from transmittances (Middleton *et al.*, 1997a).

The species bias in the blue spectrum should be considered in future improvements of algorithms to estimate leaf area in conifer stands using this methodology (Chen 1996 a,b). Furthermore, since blue adaxial reflectance provided the best separation of boreal tree species, even considering seasonal changes, this spectral region should be important in remote sensing of boreal landscapes to classify species distributions.

References

Carter, G. A., K. Paliwal, U. Pathre, T. H. Green, R. J. Mitchell and D. H. Gjerstad. 1989. "Effect of competition and leaf age on visible and infrared reflectance in pine foliage", *Plant, Cell and Environ.*, Vol. 12, pp. 309-315.

Chen, J. M. 1996a. "Canopy architecture and remote sensing of the fraction of photosynthetically active radiation in boreal conifer stands", *IEEE Transactions on Geoscience and Remote Sensing*, Vol. 34, pp. 1353-1368.

Chen, J. M. 1996b. "Evaluation of vegetation indices and a simple ratio for boreal applications", *Canadian J. Remote Sensing*, Vol. 22, pp. 229-242.

Chen, J. M. and S. G. Leblanc. 1997. "A four-scale bidirectional reflectance model based on canopy architecture", *IEEE Transactions on Geoscience and Remote Sensing*, Vol. 35, pp. 1316-1337.

Daughtry, C. S. T., L. L. Biehl, and K. J. Ranson. 1989. "A new technique to measure the spectral properties of conifer needles", *Remote Sensing of Environment*, Vol. 27, pp. 81- 91.

Esau, K. 1977. Anatomy of seed plants, 2nd ed., John Wiley & Sons, NY., 550 pp.

Gausman, H.W. 1974. "Leaf reflectance of near-infrared". *Photogrammetric Engineering*, Vol. 41, pp. 183-191.

Gausman, H. W. 1982. "Visible light reflectance, transmittance, and absorptance of differently pigmented cotton leaves", *Remote Sensing of Environment*, Vol. 13, pp. 233-238.

Gausman, H. W. 1984. "Evaluation of factors causing reflectance differences between sun and shade leaves", *Remote Sensing of Environment*, Vol. 15, pp. 177-181.

Gausman, H. W., W. A. Allen, R. Cardenas, and A. J. Richardson. 1970. "Relation of light reflectance to histological and physical evaluations of cotton leaf maturity", *Applied Optics*, Vol. 9, pp. 545-552.

Hall, F. G., P. J. Sellers, M. Apps, D. Baldocchi, J. Cihlar, B. Goodison, H. Margolis, A. Nelson. 1993. "BOREAS: Boreal Ecosystem-Atmosphere Study", *IEEE Geosci. Remote Sensing Society Newsletter*, pp. 9-17.

Kimball, J. S., P. E. Thornton, M. A. White, and S. W. Running. 1997. "Simulating forest productivity and surface-atmosphere carbon exchange in the BOREAS study region", *Tree Physiol.*, Vol. 17, pp. 589-599.

Lavigue, M. B. and M. G. Ryan. 1997. "Growth and maintenance respiration tates of aspen, black spruce and jack pine stems at northern and southern BOREAS sites", *Tree Physiology*, Vol. 17, pp. 543-551.

Loechel, S., C. Walthall, E. Brown de Colstoun, J. Chen, B. Markham, and J. Miller. 1997. "Model-based analysis of canopy and understory reflectances at BOREAS", *J. Geophys. Res.*, in press.

Mesarch, M. A., E. A. Walter-Shea, G. Asner, E. M. Middleton, and S. S. Chan. 1998. "A revised measurement methodology for conifer needle spectral optical properties", *Remote Sens. Environ.* (submitted 8/98).

Middleton, E. M., S .S. Chan, M. A. Mesarch, and E. A. Walter-Shea. 1996. "A revised measurement methodology for optical properties of conifer needles", *Proceedings, 1996 Internat'l Geoscience and Remote Sensing Symposium* (IGARSS'96), 5 pp.

Middleton, E. M., E. W. Chappelle, and A. DeLuca. 1995. "Evaluating photosynthesis in boreal forest species with fluorescence measurements", *Proceedings, 1995 Internat'l Geoscience and Remote Sensing Symposium* (IGARSS'95), pp. 1723-1725.

Middleton, E. M., S. S. Chan, R. J. Rusin, and S. K. Mitchell. 1997a. "Optical properties of black spruce and jack pine needles at BOREAS sites in Saskatchewan, Canada", *Canadian J. Remote Sensing*, Vol. 23 (2), pp. 108-119.

Middleton, E. M., J. H. Sullivan, B. D. Bovard, A. J. DeLuca, S. S. Chan, and T. A. Cannon. 1997b. "Seasonal variability in foliar characteristics and physiology for boreal forest species at the five Saskatchewan tower sites during the 1994 Boreal Ecosystem-Atmosphere Study (BOREAS)", *J. Geophys. Res.*, in press.

Middleton, E. M. and E. A. Walter-Shea. 1995. "Optical properties of canopy elements in the boreal forest," *Proceed. 1995 International Geoscience and Remote Sensing Symposium (IGARSS'95)*, Library of Congress No. 95-75916, Firenze, Italy, pp. 789-793.

Miller, J. R., H. P. White, J. M. Chen, D. R. Peddle, G. McDermid, R. A. Fournier, P. Shepherd, I. Rubinstein, J. Freemantle, R. Soffer, and E. LeDrew. 1997. "Measurement of seasonal change in the mean understory reflectance for boreal forests and its application to determination of canopy vegetation indices", *J. Geophys. Res.*, in press.

Myneni, R. and D. L. Williams. 1997. "A canopy reflectance model for coniferous forests and its validation", *J. Geophys. Res.*, in press.

Norman, J. M. and P. G. Jarvis. 1974. "Photosynthesis in Sitka Spruce (Picea Sitchensis (Bong.) Carr.) III. Measurements of canopy structure and interception of radiation", *Journal of Applied Ecology*, Vol. 11, pp. 375-398.

Rock, B. N., D. L. Williams, D. M. Moss, G. N. Lauten, and M. Kim. 1994. "High-spectral resolution field and laboratory optical reflectance measurements of red spruce and eastern hemlock needles and branches", *Remote Sensing of Environment*, Vol. 47, pp. 176-189.

Running, S. W., R. B. Myneni, R. Nemani, and J. Glassy. 1996. "MODIS Lai/fPAR algorithm theoretical basis document, *ftp://eospso.gsfc.nasa.gov/ATBD/REVIEW/MODIS/ATBD-MOD-15/atbd-mod-15.pdf.*

Sellers, P. J., *et al.* 1995a. "The Boreal Ecosystem-Atmosphere Study (BOREAS): An overview and early results from the 1994 field year," *Bull. Amer. Meteorol. Soc.*, vol. 76, pp. 1549- 1577.

Sellers, P. J., J.A. Berry, G.J. Collatz, C. B. Field, and F. G. Hall. 1992. "Canopy reflectance, photosynthesis, and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme," *Remote Sens. Environ.*, vol. 42, pp. 1-30.

Sellers, P. J., F. G. Hall, D. Baldocchi, J. Cihlar, P. Crill, G. den Hartog, B. Goodison, R. D. Kelly, D. Lettenmeier, H. Margolis, J. Ranson, and M. Ryan (editors), 1995b. *BOREAS Experiment Plan*, Ver. 3.1 (May 1995), NASA/Goddard Space Flight Center, Greenbelt, MD.

Sellers, P. J., F. Hall, H. Margolis, B. Kelly, D. Baldocchi, G. den Hartog, J. Cihlar, M. G. Ryan, B. Goodison, P. Crill, K. J. Ranson, D. Lettenmeier, and D. E. Wickland. 1995c. "The Boreal Ecosystem-Atmosphere Study (BOREAS): An overview and early results from the 1994 field year", *Bull. Amer. Meteorol. Soc.*, Vol. 76, pp.1549-1577.

Sinclair, T. R., R. M. Hoffer, and M. M. Schreiber. 1971. "Reflectance and internal structure of leaves from several crops during a growing season", *Agronomy Journal*, Vol. 63, pp. 864- 867.

Steele, S. J., S. T. Gower, J. G. Vogel, and J. M. Norman. 1997. "Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada", *Tree Physiology*, Vol. 17, pp. 577-583.

Sullivan, J.H., B.D. Bovard, and E.M. Middleton. 1997. "Variability in leaf level CO_2 and water fluxes in *Pinus banksiana* and *Picea mariana* in Saskatchewan", *Tree Physiol.*, Vol. 17, pp. 553-562.

Thomas, J. R. and H. W. Gausman. 1977. "Leaf reflectance vs. leaf chlorophyll and carotenoid concentrations for eight crops", *Agronomy Journal*, Vol. 69, pp. 799-802.

Walter-Shea, E. A. and J. M. Norman. 1990. "Leaf optical properties", In: R. B. Myneni and J. Ross (Eds.), *Photon-Vegetation Interactions: Applications in Optical Remote Sensing and Plant Ecology*, Springer-Verlag, New York, pp. 229-251.

Walter-Shea, E. A., J. M. Norman, and B. L. Blad. 1989. "Leaf bidirectional reflectance and transmittance in corn and soybean", *Remote Sensing of Environment*, Vol. 29, pp. 161- 174.

Wang, K., Kellomaki, S., and Laitinen, K. 1995. "Effects of needle age, long-term temperature and CO_2 treatments on the photosynthesis of Scots pine", *Tree Physiol.*, Vol. 15, pp. 211- 218.

Williams, D. L. 1991. "A comparison of spectral reflectance properties at the needle, branch, and canopy level for selected conifer species", *Remote Sensing of Environment*, Vol. 35, pp. 79-93.

Wooley, J. J. 1971. "Reflectance and transmittance of light by leaves", *Plant Physiology*, Vol. 47, pp. 656-662.